Seed Production in *Pinus radiata* D. Don: Impact of Climate and Site on Numbers of Emergent Female Strobili

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ABSTRACT

This thesis describes a study undertaken to improve the capacity of seed orchard managers to select productive sites for the production of *Pinus radiata* seed. It is applied in its approach, with the major intent being to explore the relationship between environmental variables, and numbers of emergent female strobili at anthesis.

Following the development of a sampling methodology for counting strobili, data were collected from 52 open grown stands of *Pinus radiata* ranging in age from 10 to 12 years located over a range of latitudes and altitudes east of the main dividing range of the South Island. Stands were selected to be reasonably close to a meteorological station.

Based on existing knowledge of when environmental variables impact on the numbers of strobili carried at the time of anthesis, monthly temperature and water stress data for the spring months of the year prior to anthesis, and also for subsequent summer months, were correlated with numbers of strobili across sites. Winter temperatures prior to anthesis were also correlated with the strobilus data.

The variables that were significantly correlated with strobilus number were then included in a stepwise multiple regression analysis with the intent of developing a statistical model for strobilus production. The multiple regression analysis selected the following variables into the model equation (with the percentage of the variance accounted for by each variable shown in brackets):

(i) Mean minimum temperature for February (around the time of seed-cone bud differentiation) (54%).

(ii) Integrated soil water stress for February and March (6%).

(iii) Accumulated growing degree days weighted against rainfall for the spring prior to seed-cone bud differentiation (4%).

(iv) Mean minimum temperature for May (between differentiation and anthesis) (1%).

Overall the model was able to account for around 65% of between-site variability in strobilus

number. The model variables suggested that predominantly temperature and to some extent rainfall govern the number of seed-cone buds that begin differentiating; and the number that finally reach anthesis in the spring. Two years later in 1994 the statistical model was validated across 12 new South Island sites. It was found that the model estimates were in close agreement with actual counts, with 75% of the residual values falling within the 95% confidence limit bounds.

Considering that mean February temperature was so highly correlated with strobilus number it was considered appropriate, whilst validating the model in the South Island, to extend sampling into the North Island. 11 stands were sampled, situated along both east and west coasts, where warmer summer temperatures prevail. However, the model estimates were less accurate in the North Island than the South. Both the data for 1992 and 1994 (total 74 sites) were combined and strobilus data were remodelled. Again the multiple regression analysis selected the mean minimum temperature of February as the variable that explained most of the between-site variance. The mean number of strobili at sites in the North Island was 1.4 times greater than that for the sites in the South Island, with trees at the best North Island site carrying 38% more strobili than those at the best site in the South Island.

Considering that long-term data for the February temperature variable were readily available and that the relationship between temperature and strobilus production is likely to have an upper-limit, the Schumacher sigmoid growth function was fitted to the strobilus data for the 74 sites in the both the 1992 and 1994 studies. This function was found to satisfactorily describe the relationship between strobilus number and February temperature, although due to the lack of data points at the high end of the temperature range, the response curve was not typically sigmoid with a flattening off at higher temperatures.

Using both a GIS mapping system and a climate surface model, mean minimum February temperatures for New Zealand were mapped to assist with the selection of potential seed orchard sites.

It was apparent from the maps that prime sites for strobilus production are likely to be those that have a mean minimum February temperature >15°C, and that those sites tend to be on northern coastal headlands and capes with insular climates. The majority of the sites meeting the temperature criteria are in the North Auckland region. It is likely that a reproductive environment for *Pinus radiata* is one where the temperature does not vary greatly, either diurnally or seasonally.

Assessments of conelet abortion and cone seed yield and weight, made at the time of counting strobili, showed that the levels of conelet abortion were independent of the numbers of strobili carried by trees. Seed weight was also unrelated to strobilus production, but seed number was correlated. The high strobilus-producing sites tended to yield more full seeds per cone.

To verify the significance of the variables in the statistical model experimental studies were undertaken using clonal graft material at Amberley seed orchard, Canterbury.

Firstly, an experimental study confirmed the importance in the model of February as a time to influence strobilus numbers. Grafts put into a low-intensity-light building for 2 week periods during February and early March produced no strobili the following spring, while strobilus production was unaffected on grafts moved at other times between January and the 26th of March.

In a further experiment, cooling grafts during the summer months reduced the number of strobili per whorl by 44% and the number of grafts carrying strobili by up to 80%. Siting grafts at cool inland sites during the winter on the Canterbury plain caused a loss of up to 61% in seed-cone buds. However, neither warming grafts in a polyethylene house during long shoot primordia initiation/differentiation; or in a heated glasshouse during the winter months leading up to anthesis, increased strobilus production. The reasons for this are discussed. In hindsight it would appear that the maximum temperatures in the polyethylene house were too high for strobilus production, whilst in the heated glasshouse there was insufficient diurnal temperature variation, along with an interruption to the normal seasonal cooling pattern. Nonetheless, considering both the site predictions of the strobilus model and findings of these experiments it is proposed that an optimal reproductive environment for radiata pine is probably one where warm temperatures are relatively constant and do not vary greatly diurnally or seasonally.

Summer soil water stress was implicated with strobilus production, although to a lesser extent compared to mean minimum February temperature. That is, the sites more water stressed during February and March tended to produce more strobili than those that were less water stressed. This effect was borne out by an irrigation pot trial in 1993 which showed that irrigation reduced the numbers of strobili carried by grafts by up to 45%. However, due to persistent summer rain this effect was not satisfactorily demonstrated in an irrigation field trial conducted at Amberley seed orchard.

The temperature and moisture conditions during the spring of the year prior to anthesis were found to indirectly impact on strobilus production by modifying the number of branches produced by grafts. When graft shoot growth was increased by modifying spring growing conditions, more branches developed per whorl.

Finally, the effect of nitrogen fertiliser applications on strobilus production was tested across a range of sites and climates. There was no significant direct effect of N-fertiliser on strobilus production, regardless of N-form applied. It is unlikely that the use of nitrogen fertilisers in a well managed radiata pine seed orchard will enhance strobilus production; or that the inclusion of a soil-N variable in the model would improve its predictability.

The statistical model developed in this thesis has added to knowledge regarding the identification and the importance of site environmental variables associated with female strobilus production in *Pinus radiata*. Further the model identified mean minimum February temperature as a key variable, for which long term data is readily available across New Zealand. These data were used to construct 2 mean minimum February temperature maps for New Zealand which can now be used to assist with seed orchard site screening. Experimentally it was demonstrated that temperature and moisture conditions govern the number of seed-cone buds that are differentiated and reach anthesis. It is recognised that environmental variables can impact on strobilus formation in both direct and indirect ways.

The possibilities for extending the databases developed in this thesis to develop further understanding of seed production processes is advocated.

CHAPTER I

GENERAL INTRODUCTION

Traditionally, most research into the seed production of commercially-grown forest tree species has been in connection with genetic improvement programmes. The research reported in this thesis is no exception. Its prime objective was to contribute to an improvement in the yields of genetically improved seed from control pollinated seed orchards.

Classically in conifers, clonal seed orchards have been used as the output systems for genetically improved material from breeding programmes. While seed orchards are by no means the only available output systems, they are biologically and logistically simple to operate, and are in widespread use for that reason.

There has been considerable development in seed orchard technology since the original concept was proposed by Syrach Larsen in 1956. In the original concept, orchards consisted of randomised ramets of a number of clones. It was expected that the female strobili on any ramet would have an equal opportunity of being pollinated by the pollen of any other ramet; and that careful placement of ramets would reduce the incidence of self pollination. The presence of outside pollen would be reduced by having a substantial isolation barrier around each orchard.

With the passage of time, considerable limitations were recognised for such orchards. These were first critically articulated by Sweet and Krugman (1977), and since that time clonal orchards of *Pinus radiata* (radiata pine) in New Zealand have been substantially modified in form. All new orchards in New Zealand are now control-pollinated (CP) "meadow" orchards. In a meadow orchard, high numbers of stems per hectare (currently 3,300) are managed intensively for cone production for short rotations of 5 to 7 years (see Plate 1.1). A key part of the management is the planting of ramets in clonal blocks, and applying a pruning regime which will allow all operations to be carried out from the ground. The development of the present system has been well reported by Carson, Vincent and Firth, (1992).

Because of the need to work from the ground, an important requirement of a meadow orchard is for ramets to initiate strobili shortly after establishment, and while they are small in size. This requires the use of sites which are very conducive to strobilus initiation. A further reason to use sites which are very favourable for reproduction is the requirement to obtain seeds from clones which are variable in their reproductive capacity. Observations suggest that on "good flowering" sites, the number of clones carrying heavy cone crops is considerably higher than on "poor" sites.

The extraction of mature seed from seed orchard cones is the last step in a long series of biological and management events commencing with the initiation of strobili, and incorporating the processes of pollination, fertilisation and seed development. The developmental processes of seed production in radiata pine are well understood (see e.g., Sweet and Bollmann, 1971; Bollmann and Sweet, 1976; Lill and Sweet, 1976). There are a number of places where losses of potential seed occur (see e.g., Sweet, 1973 and Figure 1.1); and thus any two sites which initiate the same number of strobili will not necessarily produce the same number of mature seed. However, because the starting point of the process is the initiation of strobili, and because of the specific requirements of meadow orchards, it is vital for seed orchard managers to have some understanding of the factors which influence the initiation of reproductive structures.

Knowledge to date of variation in female strobilus production of radiata pine in New Zealand places a high significance on the importance of site. Data collected by D.S. Jackson (unpub.) and reported by Sweet (1975) is presented in Figure 1.2 to illustrate that point. The data in Figure 1.2 is in fact based on cone counts, and some of the variability may thus incorporate site differences in the incidence of conelet abortion (Sweet and Thulin, 1969). But the overall impact of site on reproduction is striking.

The siting of past and current radiata pine seed orchards in New Zealand has been based largely on pragmatic factors. Suitable pollen isolation was a key factor for early open-pollinated orchards, and within that constraint, companies aimed to place their seed orchards on land close to their operations. Thus an analysis of existing orchards, while showing considerable variability in cone production, gives indications only as to where future orchards should (and should not) be located. Today, 3 existing control-pollinated orchards occur in the Bay of Plenty region of the North Island (at Te Teko, Onepu and Matakana); 3 in the Marlborough region of

the South Island (Wairau Valley and Seddon); and 2 in Canterbury in the South Island (Amberley and Waikuku) (see Figure 1.3).

To a lesser extent the data in Figure 1.2 also failed to provide a clear lead on orchard siting. The data were collected (in the 1960's) from areas representing the then distribution of radiata pine in plantations. They did not sample the country as a whole, and initial attempts from that study to relate the variability in cone counts to climate and soils were not successful. The raw data from that study are no longer available, and thus it has not been possible to analyse that data further in this thesis.

One of the highest cone-producing areas shown up in the study illustrated in Figure 1.2 was the Bay of Plenty. The Forest Research Institute initiated trials in that area in the 1970's, to try to obtain further information on the relationship between climate and cone production; but the (unpublished) results showed large variation in strobilus number within a region, which were not easily explainable in terms of climate or soils.

Further, the control-pollinated orchards in the Bay of Plenty are not regarded as being amongst the highest-producing in the country. In fact, the correlation between known orchard productivity and the data in Figure 1.2 proved to be only moderate.

Thus in 1992 when this research started, there was a strong acceptance by seed orchard managers of the importance of site in terms of meadow orchard management; but a lack of real knowledge as to where future orchards should be sited. This study thus set out to determine how radiata pine female strobilus production relates to site and climate in a broad sense. The classical way to obtain such information is to undertake a survey of a range of areas whose reproductive capability is known to be variable and whose sites can be characterised; and to develop a mathematical relationship to explain the variability. This study did that, and also set out to test experimentally the effect of the climatic parameters indicated as important by the model.

In the initial chapters, surveys will be reported recording patterns of female strobilus and seed production across a range of coastal and inland sites along the eastern part of the South Island of New Zealand . A multiple regression model that explained around 65% of the variability in strobilus production patterns across those sites will then be presented. The validation of that

model will then be described followed by the prediction of sites in New Zealand as a whole that have the potential to produce high numbers of female strobili.

The initial survey studies provided information on some of the primary site and climatic variables associated with the initiation of strobili. Clonal material was then used in a series of experiments to test the significance of these. Those experiments, comprising mainly air temperature (spring, summer and winter) and summer soil water-stress effects, will be described in the experimental chapters of the thesis.

Finally the overall findings of this study, along with a consideration of potential areas for further research, will be reviewed in the General Discussion.

The study was a very applied one in its approach. Its primary aim was to enable orchard managers to increase yields of genetically improved seed from meadow orchards; rather than to increase scientific understanding of the reproductive process in *Pinus per se*. Nonetheless, some of the findings do inevitably contribute to basic knowledge in that area.

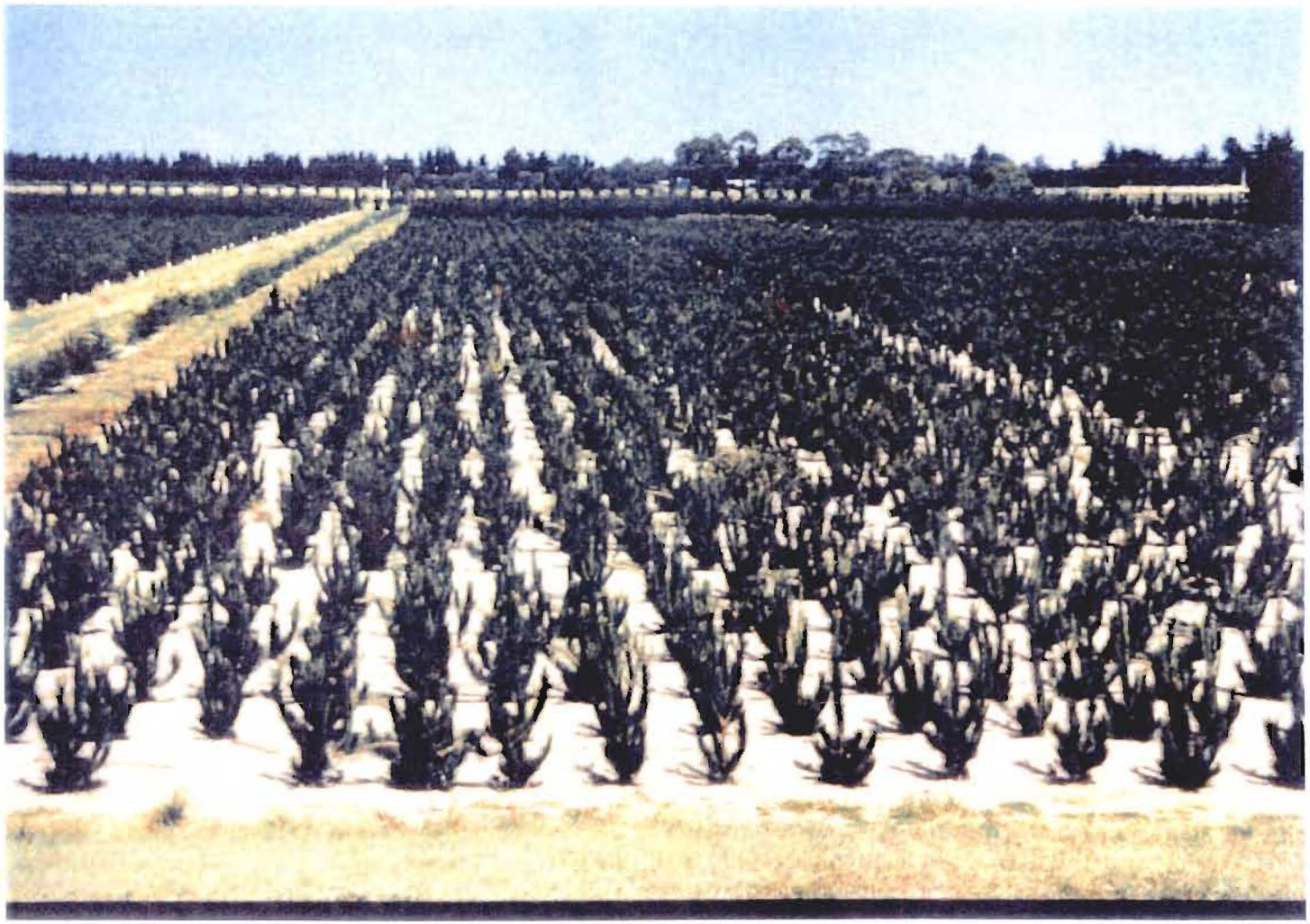

Plate 1.1

A view of 2-year-old *Pinus radiata* grafts in a clonal meadow-orchard block at Amberley seed orchard. The planting density is 3,300 stems per ha^{-1}.

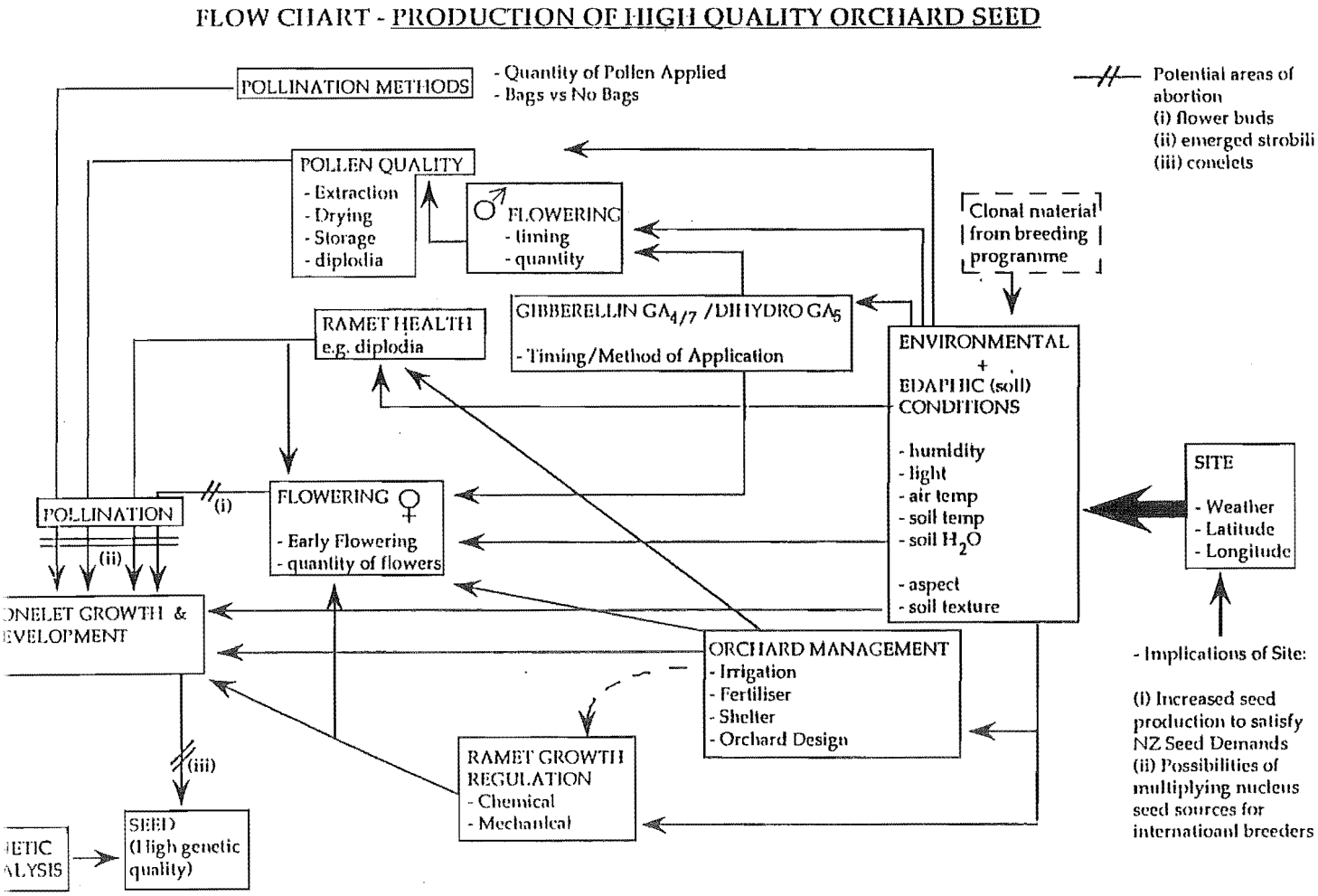

Figure 1.1

Flow chart illustrating the various interdependent factors, and steps, involved in the production of high quality control-pollinated radiata pine seed.

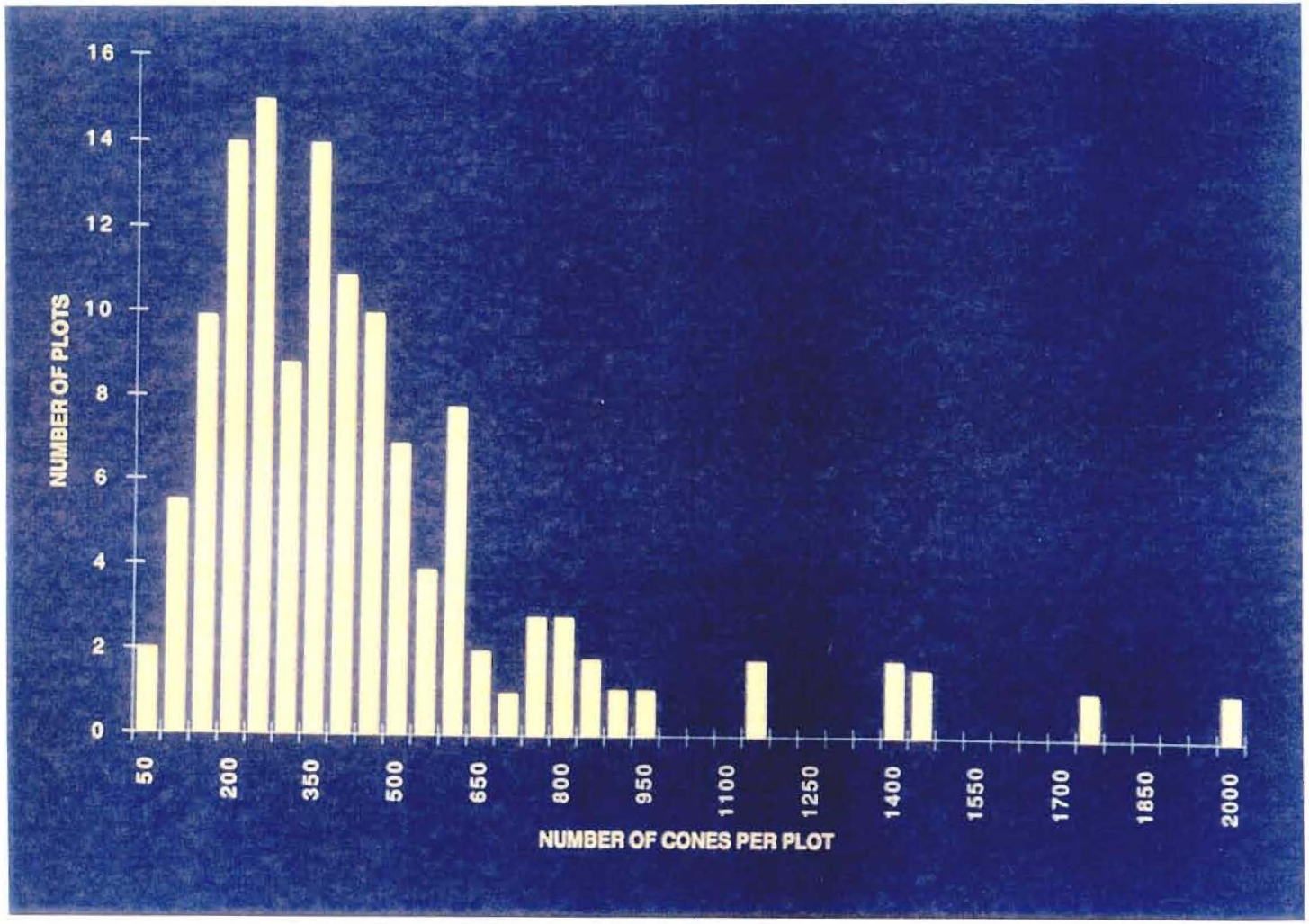

Figure 1.2

Frequency distribution histogram of cone production of radiata pine, on 129 sites in New Zealand. This figure is reproduced from Sweet (1975).

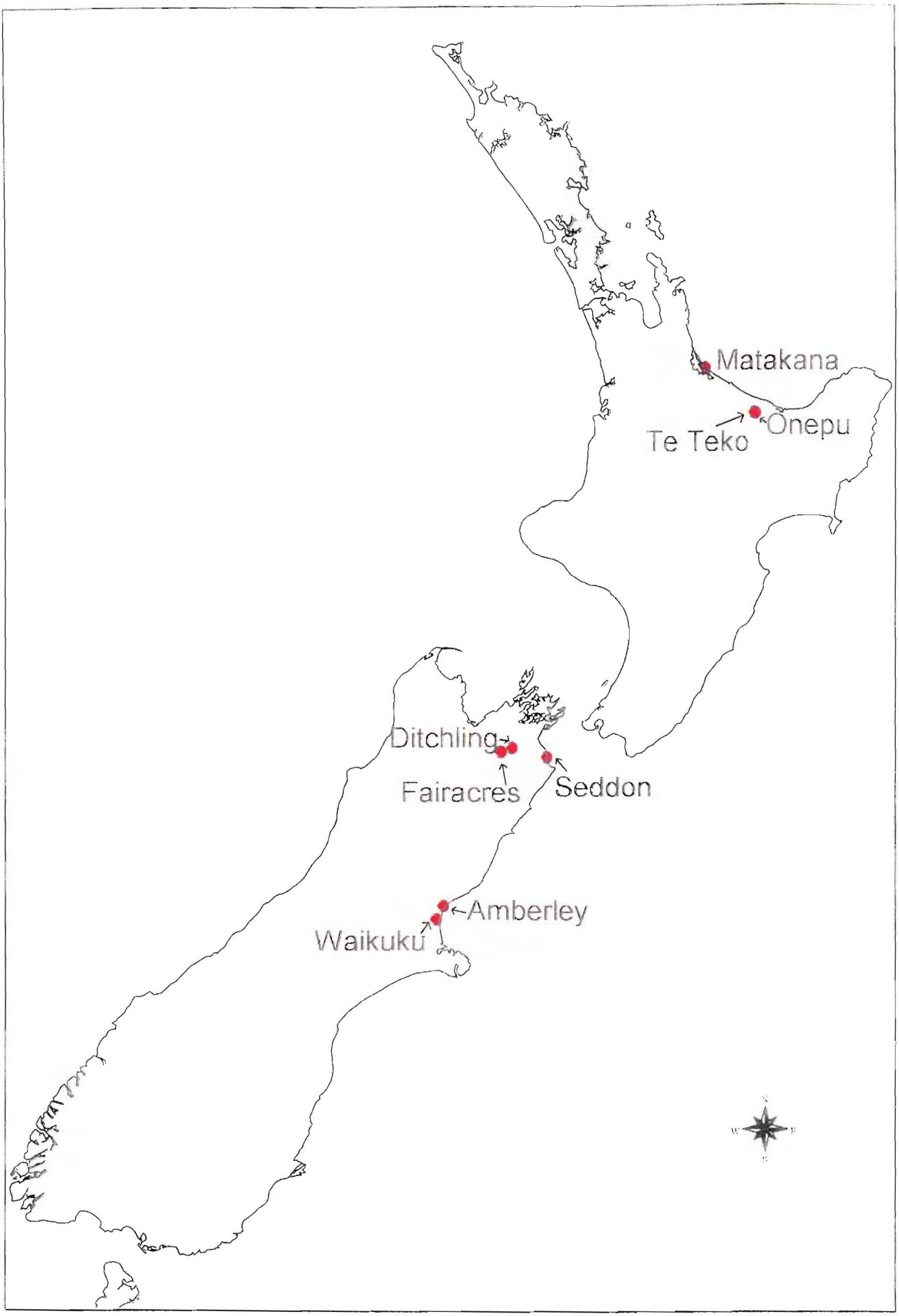

Figure 1.3

A map illustrating the location of the existing control-pollinated seed orchard sites in New Zealand.

CHAPTER 2

LITERATURE REVIEW

A. INTRODUCTION

The flowering literature is vast, and the issue in a review such as this lies in determining how much of it, and which part, is relevant. Jackson and Sweet (1972) in facing that problem, proposed a division of flowering plants into two groups; those which initiate flowers in response to specific stimuli, such as photoperiod or vernalization; and those whose flowering is not so precisely controlled. They placed most woody perennial plants, and specifically conifers, in the later group.

This review will accept that approach, and will restrict the literature it reviews accordingly.

B. TERMINOLOGY

As pointed out in several papers on reproduction in conifers, there is a need to be clear regarding the definition of terms used, and there is not consistency in that respect in practice.

Jackson and Sweet (1972) referred to the difficulty of using the term "flowering" when the most commonly used definition of a flower (a determinate sporogenous shoot bearing carpels) excludes the strobili of gymnosperms. They thus re-defined a flower as "a determinate sporogenous shoot", thereby making it possible to use the term coniferous flower.

Although quite acceptable it was decided for academic reasons that the term **strobilus** rather than **flower** will be used in this thesis. However, occasionally in the literature review, when comparing gymnosperms and angiosperms, the terms flower(s) and strobilus (strobili) may be used interchangeably for conifers. When this occurs the term flower is considered to be as defined in Jackson and Sweet (1972).

The research reported in this thesis is almost entirely concerned with female, rather than male

strobili. Thus in the experimental chapters of the thesis, the word strobilus(i) will be used to mean female strobilus(i) unless specifically qualified.

Further, terminological issues arise in plants whose flowering is not initiated by a single event, but in which there is a lengthy process of development. In *Pinus*, for example, meristems developing in the axils of cataphylls (primary leaves) may develop into either short shoots or long shoots. While short shoot meristems may in turn develop into either needles or male strobili, long shoot meristems may develop into branches or female strobili (Doak, 1935). Determination of the direction of development is not an instantaneous process, and the direction is reversible over quite long periods of time if the environment changes (Silen, 1973a). The terms initiation, determination and differentiation have all been used somewhat indiscriminately in the literature to cover events leading to the development of strobili in conifers.

In this thesis, only 2 of the 3 above terms will be used. The term **initiation** will be used to refer to the process of long (or short) shoot formation in the axil of a cataphyll; and the term **differentiation** to refer to the development of that long (or short) shoot into a vegetative or reproductive structure. Thus for example, an axillary meristem may **initiate** a long shoot which in turn may **differentiate** into a female strobilus.

The above usage does not utilise the term determination (Romberger, 1967) to identify the period during which a long or short shoot is "determining" whether to develop reproductively or vegetatively. That term has not received general acceptance in the literature, largely because the period of determination has been shown to be drawn out over a number of weeks and to be reversible. Rather, on the basis of morphological or physiological evidence (potentially) reproductive buds, once they have been initiated, are normally described as undifferentiated, differentiating or differentiated.

C. MORPHOLOGY OF REPRODUCTIVE DEVELOPMENT

1. ANNUAL AND PERENNIAL FLOWERING

In general, research into the reproductive biology of perennial crop plants has lagged behind that into annual agronomic and horticultural crops. Much research has concentrated on the group of annual species that flower and seed within one year, in contrast to perennial species whose flowering appears to be less precisely controlled (Jackson and Sweet, 1972).

For a number of annual plants the flowering process has been shown to be under the control of a single promotive factor such as photoperiod, where a series of long or short days (in different species) can trigger flowering.

The use of controlled environments has allowed significant gains to be made in the understanding of flowering in annual plants. Suitable conditions (primarily photoperiod and temperature regimes) can be readily created to move plants through two or even three generations per year. Thus experiments can be easily repeated, allowing the collation of comprehensive information on flowering. This has led to rapid gains in crop improvement via selection and breeding.

By contrast perennial tree species are much less easily worked with in terms of flowering research. This is because of juvenility, seasonality of flowering, and a predetermined growth habit of which flowering may be a component (see Bollmann and Sweet, 1976). A number of years work is generally required before useful results can be obtained.

Most tree species exhibit a juvenile stage, a period when the plants make active vegetative growth but will not flower or fruit. The time involved in transition to the flowering condition varies greatly from species to species, ranging from 1 year in certain shrubs to 30-40 years in forest tree genera such as *Fagus* (Wareing, 1961). Following this period, flowering begins as a potentially seasonal phenomenon. The beginning of the flowering condition does not normally lead to senescence and/or death of the plant as it does in many herbaceous plants.

In most woody tree species gross seasonal changes appear to be important for flowering. In temperate species, buds show a distinct resting period over the winter months. In tropical

species, this may be a dry season response. In some cases a period of chilling where the temperature falls below a threshold level is a prerequisite for plants to resume growth. Thus most tree species flower only once per year.

In woody perennial plants there may be predetermined growth patterns that need to be followed before floral buds can be initiated. *Pinus* is a good example of a genus where the initiation of reproductive structures is tightly linked to vegetative growth patterns. For that reason no single promotive factor is likely to be involved in strobilus initiation in *Pinus*.

Overall a combination of problems such as the size and time required to achieve the adult condition make trees difficult subjects for flowering studies. Those are further compounded by the logistical difficulties of placing mature flowering plants in controlled environments, because of their size.

2. WOODY PERENNIAL PLANTS

2.1 Floral Bud development

The transition to the flowering condition is essentially the same in both angiosperms and gymnosperms in that an indeterminate vegetative shoot is transformed into a determinate reproductive shoot.

From the time of initiation, reproductive buds are enclosed in a protective cover comprising a series of scales and bracts. Buds not protected by such structures are uncommon in temperate woody plants.

Reproductive buds may be formed terminally on shoots or laterally in the axils of leaves. Plants in the Cupressaceae and Taxodiaceae are examples of those that have terminal flowering; whilst *Betula, Populus, Eucalyptus* and coniferous genera such as *Pinus* and *Pseudotsuga* have lateral flowering.

In plants that have terminal flowering leaf production gives way to the development of protective bud scales, leaf primordia and bract scales, in that order (Jackson and Sweet, 1972). Flower primordia then form in the axils of bracts, as well as at the apex of the bud.

Buds may be initiated while the vegetative shoot is still extending, or while it is inactive (Sweet, 1975). In *Pinus*, and possibly in all conifers with predetermined growth, primordial initiation does not occur in conjunction with rapid shoot extension growth.

Following initiation, development of the floral bud may be rapid and uninterrupted or slow; often with the interruption of a dormant phase. Grainger (1938) defined three classes of temperate zone plants based on floral initiation and development. They were as follows:

(a) **Direct flowering plants** - where the processes from initiation and differentiation of flower buds through to anthesis occur without interruption. This class comprised mostly herbaceous plants, along with some woody perennials.

(b) **Indirect flowering plants** - which had a period of rest (dormancy) at some time between floral initiation and anthesis. In this class nearly all temperate forest trees and some woody perennials were included along with some herbaceous plants.

(c) **Cumulative-flowering plants** - which formed floral primordia over a long period of time prior to anthesis. This class included many herbaceous plant species.

Examples of woody tree species that would be classed as direct flowering plants are the family Cupressaceae. Owens and Pharis (1967), for example, have shown that morphological development of the male strobili in the Cupressaceae can be completed in less than 20 days from initiation, and of the female strobili in less than 30 days.

Trees with slow and often interrupted development (indirect-flowering) include apple, pear and stone fruits, and the coniferous genera *Pinus* and *Pseudotsuga*.

2.2. Shoot Extension Growth

The majority of woody plants do not initiate flower buds while making active shoot extension growth. In some fruit species flowers are borne on spur shoots which make only minimal annual extension growth.

Two factors contribute to the growth of a shoot; firstly the proliferation from the apical meristem of nodes and their associated leaves, and secondly the extension of internodes which separate the nodes.

Often there exists a negative correlation between internode length and flowering (e.g. Sweet, 1975). For example, low light intensity increased internode length and reduced flower initiation in apricots (Jackson, 1969). Conversely, the application of growth inhibitors has been found to promote flowering; e.g., Alar (succinic acid 2, 2-di-methylhydrazide) applications to apples were found to reduce internode length and in turn increase flowering (Edgerton and Hoffman, 1965).

However, the negative relationship between internode length and flowering is not absolute. In the family Cupressaceae, gibberellins increase both stem elongation and flowering (Ross, Pharis and Binder, 1983). Similarly, at some tree seed orchard sites fertiliser applications increase growth (primarily crown growth) and in turn increase strobilus production (Puritch, 1972).

On the basis of the conflicting reports on shoot growth and flowering it was proposed by Sweet (1975) that although restricted growth during the time of flower initiation may favour floral activity it does not imply that restricted growth during the whole growing season does.

Heavy flowering is probably correlated to some extent with the numbers of nodes present on a tree, as these in turn control opportunities for floral buds to be initiated. Once nodes are produced, however, other factors may determine the number of floral buds produced at each node, e.g., water availability, soil nitrogen level or temperature (Jackson and Sweet, 1972). For *Pinus radiata* Bollmann and Sweet (1976) noted that the more cycles of growth a tree initiates during the growing season, the more opportunity there is for seed-cone bud differentiation to occur. It follows that the level of strobilus initiation depends firstly on the ability

of the tree to proliferate nodes (potential flower bearing sites) and secondly to initiate seed-cone buds at those nodes.

2.3 Periodicity of Flowering

Many tree species produce seed crops in a rather erratic way, alternating bumper crops (in years known as mast years), with several years when productivity is low or absent (Fenner, 1985). The process is known as mast seeding. If, as in many fruit trees, good crops are produced biennially, the process is termed biennial bearing. Generally, periodicity is common in many broadleafed tree species (Ashton, 1975) and in the Abietaceae; but is less common in the Pinaceae, Cupressaceae and Taxodiaceae. The reproductive processes in *Pinus*, in particular, are thought to have a greater tolerance to climatic conditions than in some other genera (Fober, 1976). The interval between heavy seed crops varies from one species to another, and from place to place. Depending on location it can range from two to more than fifteen years (Ashton, 1975; Fenner, 1985).

This idea that reproduction, is controlled largely by climatic factors is supported by the observation that the period between mast years increases towards the edge of a species geographical range. In New Zealand, for example, Allen and Platt (1990) reported that the periodicity for the genus *Nothofagus* increased with altitude; with longer periods between good seed crops occurring close to the timberline.

Although the literature generally refers to periodicity of seed crops, this in turn frequently, (but by no means always) is caused by periodicity in flower crops. Many factors appear to influence the size of the flower crop in trees, but the phenomenon of periodicity has allowed researchers to look for correlated weather events.

Generally the one single meteorological factor that has been found to be the most correlated with the size of the flowering crop is temperature, primarily during the time of flower bud initiation. There are reports that, depending on species, either unusually high or low temperatures can be correlated with heavy flower crops, and thus with seed loads (Poole, 1948; Norton and Kelly, 1988).

In many species seed years have been associated with high levels of nutrient supply to developing buds (Sweet, 1975). The reproductive demands in terms of carbohydrate and mineral nutrient reserves are high in a heavy flowering year, and it is not surprising to find that biennial bearing is common in perennial tree species. There is evidence that periodicity is much reduced on certain sites, and these may well be ones on which maximum carbohydrate production occurs (Matthews, 1963).

Another factor contributing to periodicity may be the lack of available flower-bearing sites. In conifers where female strobili are initiated in place of branches, a heavy flower crop must impact on the potential number of flowering sites for the next year. Matthews (1963) stated that this was the case for Norway spruce, balsam fir and radiata pine; and indicated that it undoubtedly also applies to other species in which cones are substituted for vegetative branches.

3. CONIFERS

In most temperate areas of the world commercial forestry is concerned more with gymnosperms than with angiosperms, and for that reason the majority of the forest tree literature on flowering relates to conifers.

3.1 Floral Bud Development

The processes of floral bud initiation and differentiation have been described by Owens and Blake (1985) for many north-temperate conifers. Figure 2.1 in that publication (Owens and Blake, 1985) provides good information on the timing of initiation of male and female buds in the main genera of conifers they examined. The information presented in this section unless otherwise referenced, is from Owens and Blake (1985).

3.1.1 Pinus

Female strobili differentiate from long shoot primordia (potential branch buds); and male strobili differentiate from short shoot primordia (potential needle fascicles).

3.1.2 Tsuga and Picea

In *Tsuga* generally, female strobili result from the transition of an existing terminal vegetative apex. While male strobili may also be initiated this way, they are more frequently initiated from previously undifferentiated axillary primordia.

Both these types of differentiation also occur in *Picea*, but the terminal origin predominates for female strobili, and the axillary one for males.

3.1.3 Pseudotsuga, Abies and Larix

Strobili of both sexes develop from previously undifferentiated axillary primordia. The female strobili tend to develop from distal primordia that would normally become vegetative branch buds; and male strobili from proximal primordia that would otherwise abort or remain latent.

Similarly in *Abies*, both female and male strobili develop from axillary undifferentiated primordia.

In *Larix*, strobili of both sexes generally occur on short (dwarf) shoots.

Generally (but not universally), conifers initiate and differentiate male and female strobili during the summer period prior to anthesis. Anthesis occurs in the spring, following a period of winter dormancy.

Nearly all of the evolutionarily more recent conifers are monoecious, although within species there may be certain genotypes that produce predominantly female or male strobili. Most conifers begin to produce strobili following a period of juvenility. And ontogenetically, female flowering usually starts prior to male flowering (Giertych, 1976).

3.2 Position of Male and Female Strobili in the Crown

For most conifers male and female strobili are produced in somewhat different parts of the crown. As the tree matures and its crown increases in size, female strobili are initiated first on the strong leading shoots in the upper crown. Over time, the zone of female flowering extends outward to include the most distal vigorous shoots.

Male development occurs predominantly on the less vigorous shoots in the lower crown. As the tree ages male cone production extends upward and inwards, terminating in the middle of the crown.

The zones of male and female strobili are most pronounced in poor-flowering sites and years. In good flowering years, or at good flowering sites, female strobili can sometimes be produced at the base of the crown - close to the ground (Ross, Piesch, Portlock, 1981).

3.3 Timing of Initiation

For *Pinus, Tsuga* and genera of the Cupressaceae, male strobili on a given shoot are initiated earlier in the season than female strobili.

In the case of *Larix, Abies, Picea* and *Pseudotsuga* strobili of both sexes appear to be initiated at about the same stage of shoot development.

3.4 Interchangeability of Reproductive and Vegetative Shoot Components in Conifers

Along with examples of normal morphogenesis, there are also examples in several species of development being halted abruptly or its direction changed.

The ratio of the numbers of buds initiated and actually reaching anthesis may be variable between years (Sweet, 1975). Owens (1969) showed that while comparable numbers of buds are initiated in leaf axils of Douglas fir each year, the percentage of those reaching anthesis as strobili in successive years may be quite different.

Silen (1967) recorded a cessation in the growth of male strobili in *Pseudotsuga menziesii* around three months following initiation. The number of buds that ceased growth was positively correlated with altitude of the site. The meristem in the buds remained alive, and could be forced to grow again. Although the buds originally had male reproductive potential they resumed growth in a vegetative state.

Silen (1973a) reported that the development pathway of reproductive buds of Douglas fir grafts can be changed during any month of the bud development period. This is further supported by

the considerable literature on aberrant strobili which are partly reproductive and partly vegetative (see Bingham, Wise and Wells, 1969; Ross, Pharis and Binder, 1987; Caron and Powell, 1990). The existence of these strobili indicates the close physiological relationship between reproductive and vegetative shoots. Refer to Plates 2.1 and 2.2 for some examples of reproductive aberrations in *Pinus radiata*.

Plate 2.1

Cluster coning in *Pinus radiata* where short shoots have produced female strobili rather than needles or male strobili.

Plate 2.2

A female cone of *Pinus radiata* which did not remain determinate but continued to grow vegetatively from the apex.

4. PINUS

This literature review will now largely concentrate on strobilus development in *Pinus*, and the effect of external factors on this.

Pinus can be divided into 2 sub-genera, hard pines (diploxylon) and soft pines (haploxylon) (Owens and Blake, 1985). In the hard pines (of which radiata pine is one) long shoot bud components are differentiated in the late summer or early autumn; whereas in the soft pines distal axillary primordia differentiate immediately following winter dormancy (Owens and Molder, 1977a;b).

Pines were some of the earliest conifers to be studied in terms of floral bud development (Doak, 1935). Mature pines have a pre-determined pattern of annual shoot growth. In its simplest form, the components of one season's extension growth are initiated during late summer and autumn of the previous season as a series of primordia inside an over-wintering bud (Duff and Nolan, 1958). While there are a number of variations to the pattern (Owens and Blake, 1985), in its simplest form, one cycle of growth is initiated per year . The end of the cycle is marked by a cluster of branches and female strobili (Bollmann and Sweet, 1976). Species of pine with this growth pattern are called monocyclic, and show three sequential phases of development in the annual cycle, as follows:

(a) Initiation of primordia for the next season's extension growth.
(b) Dormancy.
(c) Extension of the primordia initiated the previous season.

In polycyclic species, more than one cycle of shoot growth is initiated during a growing season. In general, boreal species are monocyclic, and species of temperate and tropical origin tend to be polycyclic. Radiata pine in New Zealand has been noted to produce up to 5 cycles in the annual shoot.

4.1 Female Strobilus Initiation

In *Pinus radiata* a typical example of a polycyclic pine, the initiation of female strobili in the annual shoot was described by Bollmann and Sweet (1976) as follows:

"the apical meristem of a leading shoot or vigorous branch initiates bud scales in the form of sterile cataphylls and then cataphylls with axillary primordia, The majority of these primordia develop into needle fascicles. After a number of needle fascicles has been differentiated, the pattern of development changes and a series of some 12 or so long shoots is initiated. The subsequent development pathway of those long shoots may be either reproductive, vegetative or latent. They may become branches, female strobili or latent buds".

The time interval between the initiation of a long shoot primordium and its differentiation into a developing branch or female strobilus (recognisable by dissection) is around six weeks (Dickson, Riding and Sweet, 1994).

As indicated in section 3.4 there is evidence that a changing environment, even well after the time of seed-cone bud differentiation beginning, may affect the direction of bud differentiation. It seems that there are few fundamental differences between reproductive and vegetative shoots in *Pinus* (Doak, 1935). This capacity to "change direction", while obviously physiologically mediated, implies a likely involvement of external environmental factors. The study of Silen (1973a) in which grafted Douglas fir plants which were moved to a new location after the time of differentiation produced strobili, while those not moved did not; indicated a clear external effect.

4.2 Bud Development from Initiation to Anthesis

In conifers generally, the time from reproductive bud differentiation to anthesis is such that the opportunity exists, not only for changes in the development pathway of long shoot components; but for abortion of these structures to occur. Examples of papers reporting this phenomenon are Hashizume (1973) and Silen (1967).

Sweet (1973) indicated that 3-5% of differentiated female strobili initiated in *Pinus radiata* abort during the three months prior to anthesis. These strobili remained attached to the stem so long as their meristems remain alive.

5. PINUS RADIATA

As already indicated, the key papers interpreting the relationship of strobilus initiation to bud morphogenesis in *Pinus radiata* are by Bollmann and Sweet (1976; 1979). Those papers established the seasonal growth pattern of several mature radiata pine clones on several sites in the central North Island of New Zealand. Although clonal and site variation exists they defined typical times of long shoot initiation in a clone with 5 cycles of growth in the annual shoot, broadly as follows:

Commencement of initiation of cycle:

1: end of September
2: mid to end of December
3: end of January
4: end of March
5: end of June

In a clone with 5 cycles of growth in the annual shoot, there may be up to 4 cycles of strobili differentiated. Clearly, each of these cycles will have been initiated and differentiated under climatic conditions which are quite different from one another.

That fact has implications when examining the climatic conditions which favour strobilus initiation. Essentially, researchers have tended to ignore the strobili produced in cycles other than the first, and to look only at climatic events around the time of initiation and subsequent differentiation of the first cycle long shoots. The justification for this lies in the fact that perhaps 80% of strobili produced on radiata pine in New Zealand are first-cycle strobili (G.B. Sweet, pers. comm.)

Another factor which was relevant to this thesis was that all the work on the timing of long shoot initiation had been done in the central North Island. During the course of this thesis, attempts were made to determine whether that published information on timing held up for a wider range of sites than the central North Island.

D. FACTORS AFFECTING REPRODUCTIVE BEHAVIOUR

1. JUVENILITY AND MATURATION

Wareing (1959) proposed that the transition from the juvenile to the adult state be referred to as maturation, and the loss of vigour associated with the tree in its later life, as ageing. Changes due to maturation are not normally modified by vegetative propagation, whereas those due to ageing are.

This section will consider juvenility and maturation in the context of the attainment of reproductive competence, during the ontogeny of trees. All trees propagated from seed exhibit a juvenile period during which they make active growth but are not reproductively competent (Wareing, 1959). The length of the juvenile phase varies from species to species. In some plants it can be an extensive time period. For example, the bamboo (*Phyllo-stachys bambusoides*) lives for 120 years before it flowers and fruits for the first and last time (Silvertown and Rabinowitz, 1985).

Juvenility has a number of important implications for tree-crop management and breeding. In particular, the time period between seed germination and the development of reproductive capability creates an economic problem for an orchardist, and governs the rate at which a plant breeder can turnover generations.

There is now acceptance that no single criterion (such as ability to produce strobili or inability to root as a cutting) can be satisfactorily used to define a plant as mature or juvenile in condition (Sweet, 1975; Greenwood, 1992). Nonetheless, given that once a tree commences flowering that capacity is ongoing, reproductive competence has been used as an indicator of maturation status.

Apart from flowering-habit changes with maturation, other characteristics of tree growth also change, particularly growth rate and form. Juvenile plants have a higher relative growth rate than mature plants, and lower levels of apical dominance.

It appears that the length of the juvenile phase is not only under genetic control but is also affected by growth rate. The attainment of maturation has been shown to be accelerated by

conditions that stimulate continuous or vigorous or continuous growth (Wareing, 1961; Hackett, 1985). The phase change from a juvenile to a mature state appears to be closely correlated with the number of leaf nodes, and with the number of mitotic cycles which have occurred in the terminal meristem (Longman, 1987). This may be related in turn to the architecture and growth pattern of the young tree. In *Pinus banksiana,* Cecich, Kang and Chalupka (1994) reported a strong positive correlation between age of beginning to produce strobili and seedling height.

It has been suggested that juvenile trees do not produce strobili because their normal growth pattern is such that there is insufficient opportunity for them to differentiate strobilus primordia. In the shoots of juvenile *Betula* trees that formed strobili, levels of ABA were elevated (Galoch, 1985). Bonnet-Masimbert and Zaerr (1987) proposed that ABA, by reducing shoot growth, thus allowed floral initiation. On the basis of a similar proposal, Longman (1976) suggested that juvenile trees have the physiological capacity to produce strobili but are "reluctant". Longman (1987) noted that in some *Pinus* species, for example, strobilus production can start in free-grown seedlings as early as 2-3 years after planting; other species though may take 10-15 years to start producing strobili.

What role does ageing play? Wareing (1961) proposed that ageing may be important for providing suitable conditions for flowering. He noted that certain horticultural practices that check vegetative growth, such as grafting onto dwarf rootstocks and girdling, can hasten the onset of flowering in juvenile trees. It is unclear, however, whether ageing treatments hasten the process of maturation. Longman (1987) noted that treatments that stimulated flowering in juvenile trees did not affect the maturation state of those trees: if the trees were not continuously treated, then flowering stopped.

It has been widely observed across a number of species (see Jackson and Sweet, 1972) that when trees are mature to over-mature, and making very limited annual vegetative growth they tend to be very reliable, and often quite prolific in their production of flowers and fruit. This aging phenomena has been associated in its physiology with the production of "distress crops" on younger trees which are unhealthy.

It has been observed in New Zealand that "over-mature" trees of radiata pine cone heavily across a wide range of sites. Such trees seem to be much less sensitive to site effects than younger trees, and for that reason are not suited to using in a study such as this.

2. CULTURAL TREATMENTS

Both genetic selection and orchard management can be expected to influence the period between planting and seed yield in an orchard. In the past numerous physical and growth-regulator treatments have been used to induce precocious flowering in juvenile and sexually mature trees; or to enhance the flowering in sexually mature trees (Bonnet-Masimbert, 1987; Longman, 1987).

Much of the research on physical and crown management treatments to promote flowering in *Pinus* was done around 20 years ago. There are numerous papers published on treatments for a range of *Pinus* species growing either in plantation stands or seed orchards. Further, these research reports have been reviewed in a number of publications (e.g. Jackson and Sweet, 1972; Puritch, 1972; Lee, 1979; Owens and Blake, 1985; Sedgley and Griffin, 1989). Selected papers that are relatively recent and present suitable examples of the various techniques that have been used to manipulate strobilus production in pine will be discussed in this Section.

Cultural treatments fall into two categories: those that release the crown and those that modify root, stem or branch growth (Sweet, 1975).

2.1 Crown Release and Hedging Treatments

Thinning (release), branch pruning and crown hedging treatments have all been reported to promote strobilus production in conifers. Overall it is thought that crown release treatments promote strobilus production in *Pinus* by increasing the availability of water, nutrients, and particularly light to the crown (Lee, 1979). The response of strobilus production to light is more fully considered in Section 3.4.

Thinning was found to increase cone production by up to six-fold in *Pinus taeda* (Bilan, 1960). Godman (1962) reported that in *Pinus resinosa* the percentage of trees carrying cones was directly proportional to the level of thinning.

Florence and M^{c}William (1956) (cited by Owens and Blake, 1985) reported that thinning promoted flowering in *Pinus elliotti* and *Araucaria cunninghami,* but the optimal density for the number of cones per tree was less than that for the number of cones per acre. Thus they raised the question regarding optimal spacing in seed orchards and plantations to achieve maximum yields. Shearer and Schmidt (1987) found that 30- and 32-year-old *Larix occidentalis* trees produced more seed cones and pollen cones as the spacing of the stand was increased.

Pruning, particularly in *Pinus elliottii*, has been found to promote the production of female strobili (Varnell, 1969). Generally, pruning is thought to promote flowering for similar reasons to thinning. That is, through improved light and possibly water relations, thus increasing the vigour of the remaining branches.

There was one report that indicated that at high altitudes pruning increased the length of the growing season by allowing the soil to thaw earlier in the spring (Proskurjakav, 1966). This in turn stimulated increased strobilus production on the remaining branches.

In a similar effect to branch pruning, hedging of the crown of *Pinus radiata* was found to increase cone production per hectare as well as increase the ease of cone collection (Sweet and Krugman, 1978).

There are reports that phenomena which cause crown or branch trauma (injury) promote flowering (Shearer and Schmidt, 1987; Lee, 1979). In *Pinus sylvestris*, for example, insect attack of the terminal bud caused branches to carry heavy loads of strobili the following year (Wareing, 1953). Resin tapping, and damage to tree crowns and roots through logging operations, have all been reported to stimulate flowering (Lee, 1979). The situation is similar to that of "distress crops".

2.2 Root, Stem and Branch Treatments

Flowering can be promoted by grafting, girdling, root pruning, root restriction and banding (Lee, 1979). Further, there are numerous examples where growth regulators have been used to promote strobilus initiation in conifers. A good account is given by Bonnet-Masimbert (1987; 1989).

2.2.1 Grafting

Grafting has the potential to promote flowering. For example, grafting on dwarf rootstocks, grafting mature scions onto seedling rootstocks or budding in crowns of mature fruiting trees (Lee, 1979). Grafting has stimulated precocious strobilus production in juvenile scions grafted to the tops of mature pines (Mirov, 1951). Ahlgren (1972) reported that the use of mature scions for *Pinus strobus* grafts may promote strobilus production because of poor graft unions (or incompatibility) causing a partial girdling - water stress effect.

Grafting has been used throughout the world to establish seed orchards in conifers (Zobel and Talbert, 1984) and to shorten the time before the onset of strobilus production. In New Zealand, *Pinus radiata* seed orchards have largely been established with grafts, made from mature scions grafted onto seedling root stocks in designated nurseries (Carson, Vincent and Firth, 1992). Problems with graft incompatibility (Sweet and Thulin, 1973) are not significant in short-rotation meadow orchards.

Simak (1979) indicated that the position from which scion material was collected in the crown affected the reproductive ability of the graft. Those whose scion was taken from the cone-producing region of the crown bore more strobili than those whose scion originated from material lower in the crown. Earliness of flowering in grafts has been found to be affected by the age of the scion material. Greenwood (1987) found that grafts of *Pinus taeda* grafted with scions from four-year-old trees began producing strobili earlier than those grafted with scions from one-year-old trees.

Apart from scion material there is horticultural evidence that the type of root stock can affect graft flowering (see Sedgley and Griffin, 1989). Krusche and Melchior (1978) reported that the rootstock may play a role in stimulating either male or female strobili.

2.2.2 Girdling, Strangulation and Banding

Girdling, strangulation and banding treatments have all to varying extents been found to promote strobilus production in conifers and flowering in fruit trees. Puritch (1972) complied a comprehensive list of papers reporting results of such experiments.

Girdling in the form of saw cuts has been reported to be an effective treatment for promoting strobilus production in conifers (Wheeler *et. al.*, 1985; Bonnet-Masimbert, 1987; Ross and Bower, 1989; Philipson, 1992). Further, this treatment frequently has an additive effect on strobilus number when used in conjunction with other cultural treatments, particularly gibberellin applications (Ross and Bower, 1989).

Strangulation with a wire or band around the stem has been found, like girdling, to promote strobilus number, albeit to a lesser extent (Wheeler *et. al.*, 1985). Mann and Russell (1957) reported that this treatment had no effect on strobilus production in *Pinus palustris,* whilst girdling increased it by over 100%.

Compared to both girdling and strangulation, banding with a metal strip around the stem tended to be the least effective strobilus promoting treatment. Bilan (1960) suggested that in order to maintain levels of carbohydrate in the shoot that are adequate to increase reproductive activity, a severe wounding treatment such as girdling is probably required.

Girdling and banding treatments are considered to cause structural damage which is undesirable when trees are required to be kept for long term seed production (Zobel and Talbert, 1984). Girdling by a single saw cut around the stem was considered to cause branch breakage and at its worst tree death (Bower and Smith, 1961). However, semi-circular double overlapping girdles made with a pruning saw have been found to be an equally effective girdling treatment whilst being less damaging to the tree (Ebell, 1971; Wheeler *et. al.*, 1985). Subsequently, although less effective than saw cuts band girdles were found to be easier to put in place (Wheeler *et. al.* ,1985), and their wounding damage healed faster, resulting in lower strobilus abortion rates.

Other reported side effects of girdling and strangulation are reduced cone size and seed weight (Hansbrough and Merrified, 1963). However, in *Pseudotsuga menziesii* banding was found

to have no effect on filled seed per cone, full seed weight or seed germination (Wheeler *et. al.*, 1985). And recently in *Pinus radiata* seed orchard clones, strangulation with plastic ties around the stem just below one-year-old cone clusters was shown to significantly increase seed size (Setiawati, 1994).

2.2.3 Gravity and Shoot Bending

Gravity, which can be manipulated by shoot bending, affects the vegetative growth and coning in some forest trees (Longman, Nasr and Wareing, 1965; Jackson and Sweet, 1972).

Generally, horizontal branches produce fewer vegetative and more reproductive buds than more upright branches. Geotropic promotion of strobilus number, however, is not widely reported for conifers. Longman and Wareing (1958) found in *Larix leptolepis* that the more closely branches were bent to the ground the more strobili they produced. Shearer and Schmidt (1987) reported that in stands of *Larix occidentalis* both seed and pollen cones grew on pendant branches.

The reason that branch bending promotes flowering is unclear. It was reported on the basis of chromatographic analysis that changes in growth regulator content take place in the shoot of *Pinus sylvestris* during bending, and that this may be associated with female flowering (Bochurova, 1970).

In some *Pinus radiata* seed orchards in New Zealand the practice of tying down the leader of ramets one year following planting is followed. The intent is not to promote strobilus production, and there have been no obvious promotive effects of this treatment on coning (S. F. Van Ballekom, pers. comm.).

2.2.4 Root Pruning and Root Restriction

Root pruning, root restriction and transplanting treatments have been reported to increase reproductive activity in some conifers (Stephens, 1964; Silen, 1973a). The mechanism involved with the coning response to these treatments is unclear. The involvement of roots in the reproductive process is much debated (Bonnet-Masimbert and Zaerr, 1987; Ross, 1991).

Some researchers have implied that the water stress induced by root pruning induces strobilus production, whilst others propose that the removal of roots reduces the amount of strobilus-inhibiting substances that are exported to the shoot (Philipson, 1983). Owens and Blake (1985) stated that the cycle of root development is very complex and root pruning should not be regarded simply as a method of causing water stress. Further, that the existence of strobilus inhibiting substances being exported from the roots had not been satisfactorily demonstrated in forest trees.

In *Pinus taeda* and *Pinus elliottii,* root pruning has acted like other stress treatments and slowed shoot growth (Hare, 1979). This has in turn been linked to the diversion of nutrients and metabolites in the shoot into reproductive development, that would otherwise have been used for extension growth (Webber *et. al.*, 1985). Further, the latter workers proposed that in Douglas-fir root pruning elevated the concentration of the less polar gibberellins in the shoot that have been associated with reproduction (see Pharis and Kuo, 1977; Chalupka, Giertych and Kopcewicz, 1982; Dunberg *et. al.*,1983).

Lifting and transplanting trees has promoted strobilus production in conifers in a way which is comparable to root pruning. Quirk (1973) reported that in Wisconsin, cone production in *Pinus resinosa* was promoted when trees, between six and ten years old, were transferred in the spring from the ground to tubs. The procedure involved complete root pruning and subsequent root restriction. Similarly, Silen (1973a) moved ramets of *Pseudotsuga menziesii* several months following the time of seed-cone bud initiation and induced strobilus production; similar ramets that were not moved did not develop any strobili.

2.3 Growth Regulators

The use of growth regulators, predominantly gibberellins, to manipulate strobilus production in conifers is well documented. There have been well over 100 papers published on growth regulators, describing results for a variety of species, chemicals, application methods and interactions with cultural treatments.

Because this study is not primarily dealing with growth regulators, this literature will not be reviewed in any detail. Rather, reference will be made to a few papers with a reasonably complete list of research work dealing with the use of growth regulators in strobilus induction.

Gibberellins have been one of the more successful growth regulators for enhancing flowering in forest trees. Original published works on this chemical dealt with the coning responses of species of Cupressaceae and Taxodiaceae to GA_3. Subsequently, the use of the mixture $GA_{4/7}$ has proved very effective at promoting strobilus production in the Pinaceae. Today, this hormone is used on a commercial scale in New Zealand *Pinus radiata* seed orchards; in some clones it has been found to increase strobilus numbers by more than 200% (Siregar, 1994).

Research papers dealing with the successful use of the gibberellins for obtaining early and enhanced strobilus production in all three of the above mentioned families were published by Pharis and Kuo (1977); Pharis, Ross and M^{c}Mullan (1980); Wheeler, Wample and Pharis (1980); Ross, Piesch and Portlock (1981); Bonnet-Masimbert, (1987) and Bonnet-Masimbert, (1989). A paper listing references to the use of growth regulators along with various cultural treatments for promoting strobilus production in conifers and flowering in broadleaves was published by Philipson (1990).

Although other growth promoters (e.g., auxins) and growth retardants (e.g., ABA) affect flowering in some orchard trees and woody ornamentals (Jackson and Sweet, 1972), there are few reports implicating their involvement with reproductive activity in forest trees. Generally growth regulators that were found to affect coning positively, worked in synergy with gibberellins.

In a review by Puritch (1972) the application of growth promoters to initiate strobilus production in juvenile conifers or enhance levels in mature ones was considered. It was concluded that auxins had a significant effect on determining the sexuality of differentiating reproductive buds as opposed to affecting the production of strobili *per se.* The direct role of auxins in floral activity, however, is uncertain (Bonnet-Masimbert, 1971).

Certain growth retardants, CCC (Chlormequat) and ABA (abscisic acid) have been found to enhance strobilus production in conifers, but again only when used in conjunction with $GA_{4/7}$ (Bleymuller, 1976; Chalupka, 1979; Ross, Pharis and Binder, 1983). Similarly, cytokinins are thought to modify the responses of conifers to gibberellin; they appear to have no effect on strobilus production on their own (Ross and Pharis, 1976).

3.0 EFFECTS OF ENVIRONMENTAL FACTORS ON REPRODUCTIVE BEHAVIOUR

In the past most information on the effects of environmental factors on coning has been obtained from studies at the forest level. Experiments have been conducted to verify the effects of some of those variables on strobilus production.

3.1 Timing

Climatic factors, primarily temperature and rainfall, appear to effect strobilus formation in *Pinus*, in common with other tree species. Although it is known from mast seeding studies that weather conditions around the time of differentiation of reproductive buds are important, there is limited experimental data on the timing of that event in pine. Few studies have established whether, for optimal floral bud development, favourable climatic conditions need to be synchronized with a particular stage of primordial development. For conifers generally however, it has been reported that the temperature during the month(s) when buds are still capable of developing either vegetatively or reproductively is significant (Tompsett and Fletcher, 1977; Tompsett and Fletcher, 1979; Ross, 1989; Ross, 1991; Adams and Greenwood, 1992; Owens, Philipson and Harrison, 1992).

Larson (1961) was able to change the flowering pattern in *Pinus banksiana* by moving potted trees into cold storage in the spring; then in the summer sequentially moving them out into a greenhouse. Thus trees at varying stages of bud development were associated with different sets of environmental conditions, primarily temperature and photoperiod.

The results indicated that when the timing of long shoot development was not synchronised with favourable environment conditions for strobilus differentiation, the number of strobili was affected. For example, trees carried fewer strobili when long shoot development occurred in the late summer, when the conditions were not conducive to seed cone-bud differentiation.

3.2 Air Temperature

Most of the information on the flowering response to temperature has been obtained from studies which relate mast seeding years to past weather records (Holmsgaard and Olsen, 1960: cited by Holmsgaard, 1972), although limited amounts have been obtained from experimental studies (Ross, 1985; 1989; 1991).

One species where reasonably complete seeding records exist, along with climate data, is European beech (*Fagus silvatica*). For example, in Denmark during a 110-year period, significant correlations were found between good seed years in beech (four classes of crop size) and climate during the time of bud initiation (Holmsgaard and Olsen ,1960: see Holmsgaard, 1972). It appeared from the regression analysis that both rainfall and temperature were highly correlated with seed yield. Similarly abundant cone crops in *Pseudotsuga menziesii*, over a 48-year period, have been significantly correlated with warm temperatures and low rainfalls (Lowry, 1966).

Further indirect evidence that temperature may play a role in flowering is that mast seeding behaviour tends to become increasingly pronounced towards the edge of a tree's geographical range (Hagner, 1965; Allen and Platt, 1990)

Interestingly, there is species variability in the temperature requirement for flowering. For example, beech, Scots pine, ponderosa pine and southern beech all mast seed in response to high temperatures. On the other hand pinyon pine (Forcella, 1981) and rimu (Norton and Kelly, 1988) are reported to require low temperatures.

Several studies have reported that pines in seed orchards located in warm climates produced more strobili than those in cool ones. Schmidtling (1987) conducted a survey on *Pinus taeda* seed production in orchards across the southern United States. The findings of that study indicated higher production in the warmer sites, for the period 1972 through to 1976. Schmidtling (1987) concluded that moving southern pine seed orchards a short distance to warmer climates increased seed yield. However, caution was expressed with regard to moving temperate pines to areas with little winter chilling, which can cause irregularities in phenology and male and female strobilus development. Physiological "after-effects" (Schmidtling, 1987) are also considered a constraint to long geographical transfers. The mechanism of these

effects, whereby the climate of an orchard influences the physiological behaviour of seedlings raised from its seed, are unclear; but they are seen as very important (Sweet, 1994).

In south-eastern Australia, Pederick and Brown (1976) found for six *Pinus radiata* seed orchards that, apart from age, environmental, genetic and cultural effects largely accounted for between-year and between-site variability in seed production. However, within the environmental component, rainfall rather than temperature was more correlated with seed yield. Unfortunately, due to the lack of data on numbers of initiated strobili across the seed orchard sites, only mature cone and seed yield data could be analysed.

In the Nordic seed orchards Eriksson (1982) found that the temperature during July in the year of strobilus initiation accounted for up to 90% of the yearly variation in seed set in both *Pinus sylvestris* and *Picea abies*. There was no apparent relationship between strobilus production and climatic factors in June of the year of initiation.

Fober (1976) showed for *Pinus sylvestris* that initiation of strobili was greatest when there was a dry and sunny spring, followed by a warm sunny summer. This research showed significant correlations between monthly temperature and seed-cone numbers. The highest correlations were for the months strobilus buds were being initiated/differentiated. Similarly, Chalpuka (1975) showed in Norway spruce significant correlations between temperature of the months of bud initiation and numbers of strobili: the correlations were even stronger for this species than *Pinus sylvestris*.

Controlled experiments have shown that the reproductive development of conifers is to a large extent dependent on temperature (Chalpuka, 1975; Chalupka and Giertych, 1977; Tompsett and Fletcher, 1977; Tompsett and Fletcher, 1979; Adams and Greenwood, 1992; Owens, Philipson and Harrison, 1992).

Chalupka and Giertych (1977) found that enclosing the crown of *Picea abies* under polyethylene covers around the time of pollen-cone bud initiation greatly increased the numbers of male strobili at anthesis. These workers acknowledged the fact that the covers may have confounded the strobilus production effects by modifying the light conditions. However, they concluded that although the covers slightly reduced light intensity, the spectrum was unchanged.

More recently Owens, Philipson and Harrison (1992) found that elevated temperatures during the time of bud initiation, and even more during the later stages of differentiation promoted coning in *Picea sitchensis*. Similarly, Adams and Greenwood (1992) found that elevated temperatures significantly promoted strobilus production in the spruces, *Picea mariana* and *Picea glauca.*

The physiological basis for the effect of temperature on seed-cone bud initiation in *Pinus* is largely unclear - Matthews (1963) suggested that the initiation of reproductive buds requires a certain minimal heat sum, higher than is necessary for the initiation of vegetative buds. It is probable also that seed-cone bud differentiation is to some extent negatively correlated with shoot extension rate. The observation by Ross *et. al.*, (1984) that more long shoot buds will follow a reproductive pathway under conditions (such as water stress) that slow shoot extension growth, allowing the diversion of assimilates to axillary and terminal buds, is an important one. Temperature may then play a role during bud differentiation by increasing the growth rate of developing primordia, which in turn may promote cone-bud differentiation (Sweet, 1979). An increase in temperature may result in an increase in mitotic activity in meristems. Moderately increased temperatures have been found to promote both cell division and possibly cell elongation in conifers (Carlson, 1985).

The production of endogenous gibberellin-like substances in response to stress such as elevated temperature, may also be responsible for the increased floral activity. Chalupka, Giertych and Kopcewicz (1982) showed that gibberellin-like substances built up in shoots of *Picea abies* trees following stress. Similarly, Pharis (1990) showed that reproductive-promotive treatments caused an accumulation of less -polar gibberellins in the shoots of trees. These gibberellin's have been shown to have more floral activity than those that are more polar in nature (Webber *et al.*, 1985). The modified gibberellin-substances may have had a direct effect on the development pathway selected by primordia.

Clearly, the findings of most of the temperature experiments for a range of conifers indicate that for optimal seed production, seed orchards should be established at sites that have warm temperatures around the time of seed-cone bud differentiation. It should be noted, however, that much of this research has been carried out in boreal forest climates. It is by no means certain that the results will be applicable to more temperate species; and questions must arise as to whether it is possible to exceed the temperature requirement for flowering?

Many woody plants including forest trees also have a chilling requirement for flowering. There is thus no evidence to suggest that elevated temperatures all year round are beneficial for flowering.

3.3 Precipitation, Irrigation and Water Stress

Rainfall, particularly in terms of its impact on soil water deficit, has frequently been reported to affect floral bud initiation.

It is likely in some climates where flowering research has been done that water stress and warm temperatures go hand in hand and that their effects on reproductive activity will be difficult to separate. In *Picea abies,* Fober (1976) found a positive correlation between strobilus production and the variables temperature, water stress and insolation; during the time of reproductive bud initiation. However, rainfall at this time had a negative effect on strobilus production. Similarly, Chalupka (1975) found the same correlations for *Pinus sylvestris,* although they were less strong.

As for temperature, there is much evidence that when low rainfall or water stress are coincident with the time of strobilus initiation they promote coning, and slow vegetative growth. However, vegetative growth is also necessary for the development of reproductive sites, and water deficits throughout the year are not desirable. A good generative site is likely to be one which has warm dry summers where trees are subjected to moderate water deficits only during the time of floral bud initiation.

For *Fagus sylvatica* it has been possible to demonstrate over a century, a correlation between dry summers and mast seeding (Holmsgaard and Olsen, 1960: see Holmsgaard, 1972). Subsequently, Holmsgaard (1972) demonstrated in a pot trial that water stress promoted flowering in this species.

Several attempts have been made to use climatic variables, along with seed orchard production data to predict suitable sites for *Pinus taeda* seed production (Gallegos, 1978). Overall, these researchers found that soil water content during the year of strobilus initiation, along with other soil physical parameters, was more related to seed yield than was temperature.

As for temperature, the literature on water stress is not consistent across all species. It appears that while flowering is promoted in some trees when water deficits are high, it occurs in others when rainfall is high and soil water deficits low. Obviously site also affects this.

There are reports that rainfall promotes coning in *Pinus radiata* (Pawsey, 1960; Pederick and Brown, 1976;). Also in Australia, Griffin, Crane and Cromer (1984) found that irrigation of seed orchard ramets in *Pinus radiata* generally increased female strobilus production. They concluded that availability of soil water before and during the initiation of strobili was crucial, particularly in years when rainfall was low. Radiata pine, being a polycyclic species, may initiate long shoot primordia which can potentially become seed-cone buds at several times throughout the summer. Thus any check to growth during this time caused by water stress may limit the number of cycles initiated, and thus restrict the opportunity for seed-cones buds to be determined.

Griffin, Crane and Cromer (1984) contend that much of the research reporting a positive flowering response to water stress has been carried out on Northern Hemisphere species that only initiate one annual cycle of strobilus primordia before entering dormancy. However, it was generally accepted that in those species vegetative growth during the pre-initiation phase was important for initiating optimal numbers of long shoot primordia; followed by water stress to switch more of those primordia to seed-cone buds.

3.4 Light and Photoperiod

It is known that for many woody plants shading reduces the initiation of flower buds (Jackson and Sweet, 1972). Insolation has been found to be correlated with strobilus production intensity in conifers (Chalupka, 1975; Fober, 1976), although in many studies light effects have been confounded with temperature effects.

It is generally accepted that flowering is associated with cumulatively large levels of light energy (Sweet, 1975). Evidence for this comes from observations of flowering occurring predominantly on edge or open grown trees; or on dominant trees in open grown stands with well lit crowns. This is further supported by the findings of a crown release study (Shearer and Schmidt, 1987).

Silen (1973b) reported that shading of branches in 40-year-old *Pseudotsuga menziesii* trees for periods during eight months of the growing season significantly reduced male and female coning, particularly during the second year of treatment.

Owens and Blake (1985) stated that the reasons why high light intensity increases floral activity is unclear; but it may offer a practical method of increasing flowering under certain conditions. Sweet (1975) referred to the impact of light intensity on the rate of photosynthesis, which in turn governs the amount of carbohydrates that build up within the crown. There has been a long-accepted perception of a relationship between the C:N ratio of shoots and their flowering capability (Kramer and Kozlowski, 1960).

Apart from light intensity, the light spectrum reaching meristematic tissues has also been proposed to affect flowering. Giertych (1981) suggests that the bud scales of *Picea abies* selectively filter incident light, only a fraction of which reaches the meristematic tissue. Pukacki, Giertych and Chalupka (1980) found that GA_3 and polyethylene cover treatments changed bud scale orientation such that they transmitted more incident light to the meristem. This was thought to be in part why those treatments promoted strobilus production.

Photoperiod does not appear to affect strobilus production in *Pinus* (Sweet, 1975; Giertych, 1981; Owens and Blake, 1985; Cecich, Kang and Chalupka, 1994). It does, however, in genera of the families Cupressaceae and Taxodiaceae (Pharis *et al.*, 1970; Sweet, 1975).

Further evidence that photoperiod probably does not affect flowering in *Pinus* is that polycyclic pines are able to initiate strobili in up to 4 cycles during the growing season; while the day length is continually changing. For example, in *Pinus radiata* at Rotorua, New Zealand (latitude 38° S), up to five growth cycles were initiated from November to March and three of these bore female strobili (Bollmann and Sweet, 1976). Yet the photoperiod would have been much longer when seed-cone buds in the first cycle were determined, than those in the second and third cycles. The observation of course also applies to climatic factors other than photoperiod.

3.5 Mineral Nutrients and Fertilisers

Generally there have been few experiments designed to establish whether mineral nutrients play a role in strobilus production in *Pinus*. Further, of the studies that have been carried out on this topic, few of them have separated the effects of nutrition on the processes of seed-cone bud differentiation, seed production and seed quality. A reasonably complete list of references on the application of fertiliser compounds to improve cone and seed production in conifer seed orchards has recently been compiled by Hugh Schooley, of the Canadian Forest Service, Ontario, Canada (Schooley, 1995).

It is generally accepted that for trees to produce strobili they need to have a growing and developing crown structure on which strobilus initiation sites can develop. The fertility of the soil needs to be at a level such that it can support active, healthy, vegetative growth. Matthews (1963) stated that all other factors being equal, trees growing on fertile sites tended to produce more seed than those on less fertile sites. This observation has also been made for *Larix occidentalis* by Shearer and Schmidt (1987). In *Pinus sylvestris* Sarvas (1962) also reported that strobilus production and seed production were better on more fertile sites.

Overall there have been few consistent coning responses to fertiliser treatments reported in seed orchards. Variability exists between species, sites, fertiliser rates and to some extent between years of treatment on the same site.

In terms of seed orchard fertiliser application research, findings on flowering and coning have been mixed. Results of fertiliser trials with various species including pines are listed in the review papers of Puritch (1972), Lee (1979) and Owens and Blake (1985). In *Pinus* , significant responses of female strobilus production to NPK fertilisers have been reported (Wesoly, Urbanski and Barzdajn, 1987).

To some extent the early literature is confused regarding nitrogen fertiliser effects (Sweet and Hong, 1978). Nonetheless, research into fertiliser and coning effects showed nitrogen to be the most important single element; with others such as phosphorous and potassium having been beneficial on certain sites.

In terms of nitrogen fertiliser application, several review papers indicate that female strobilus

production is generally increased by this nutrient (Puritch, 1972; Lee, 1979); but the timing (Schmidtling, 1975) and the form of nitrogen used (Ebell and M^{c}Mullan, 1970) was critical. Further, the mechanism involved is not well understood. In the 1970's there was a strong suggestion of a tie up between levels of the amino acid arginine in the foliage and strobilus production; but this has not been supported by subsequent work (e.g., Sweet and Hong, 1978).

In a clonal *Pinus radiata* seed orchard in Australia, Griffin, Crane and Cromer (1984) found that nitrogen fertiliser (urea) improved the seed yield by 13.8 kg seed/ha per annum. However, the nitrogen was only effective when used in conjunction with irrigation, or when there was adequate rainfall. This trial demonstrated that if a nitrogen response was going to occur there needed to be adequate soil water present. It was found that in the irrigated and fertilised plots the vegetative growth of the grafts was increased over that of the controls and this may have provided more sites in the crown for development of female strobili.

One of the first major users of fertilisers, and particularly nitrogen, in seed orchards was the North Carolina State Co-operative Tree Improvement Programme. This group recognised three stages in the life of a *Pinus taeda* seed orchard, namely graft establishment, vegetative growth (crown development) and the reproductive phase (C. B. Davey, pers. comm.).

In the graft establishment phase, phosphate fertiliser was largely used to encourage root growth and ultimately root closure. Then during the vegetative phase which lasted around 5 years, nitrogen was applied early in the growing season followed later, depending on conditions, by some phosphorus or potassium. Finally, in the reproductive phase heavy applications of nitrogen were applied.

The timing of nitrogen application in the reproductive phase was found to be critical; it was applied around one month prior to long shoot primordia initiation, a time reported by Ebell, (1972) to be critical for Douglas fir.

Not all forms of nitrogen fertiliser were found to be equally effective. It was thought (C. B. Davey, pers. comm.) that this may be because *Pinus* generally has low levels of the enzyme nitrate reductase the role of which is to convert the nitrate in the fertiliser into a form of N that can move into and be used by the foliage. Thus nitrate fertilisers were less effective at elevating shoot-N levels than were ammonium-based fertilisers.

Sweet and Hong (1978) in New Zealand carried out extensive research in *Pinus radiata* grafts and cuttings to establish whether nitrogen fertiliser applications just prior to bud initiation/differentiation promoted strobilus production. They were unable to find a significant effect of this element on strobilus production; even though the level of N in the foliage was raised to some 30% above the 1.6% regarded as limiting to vegetative growth (Will, 1978). These workers concluded that responses reported in the literature may have largely been due to the fertiliser increasing naturally low levels in the soil, and thus promoting crown growth and enabling the development of more sites for strobilus initiation.

Subsequently, Smith (1987) reported that in *Picea mariana* applications of ammonium nitrate increased female and male strobilus production. However, this response, again, was largely due to an increase in tree height and diameter.

E. THE REPRODUCTIVE "TRIGGER"

On the basis of the literature on strobilus production in conifers, it is apparent that the differentiation of strobili is a *very* complex physiological process, integrally associated with shoot growth patterns. It is unlikely that it is controlled by a single gene. A large range of cultural and environmental factors have been shown to promote strobilus production, and further, to some extent, to control sex determination.

It may be that external influences such as environmental conditions modify the physiological processes of growth and development at key times of the growing season such that the tree is able to capitalise more fully on its inherent flowering capacity. In essence these stimuli may act by switching on and off plant growth and development processes at various stages of generative development. Further, they may divert and shunt assimilates to reproductive regions of the plant at critical times. Evidence supporting this proposal is the fact that juvenile trees possibly have the "algorithm" or capacity to produce strobili; *all* that may be required is the right physiological conditions to be bought about within the plant.

Sweet (1979) drew attention to the possibility that the "decision" as to whether developing long shoot buds became reproductive or not may be due to something as biologically simple as their rate of cell division at the time of differentiation. This might be expected to be influenced by a number of the factors that are known to influence strobilus production.

F. UNIVERSAL PERCEPTION OF THE CRITERIA REQUIRED FOR A SEED ORCHARD SITE

It is widely accepted that site contributes more than any other single factor to the flowering of open-grown trees and grafts (Matthews, 1963; Andersson and Hattemer, 1975; Sweet, 1975; Werner, 1975; Somerville and Sweet, 1978; Zobel and Talbert. 1984; Enescu, 1987; Allen and Platt, 1990; Fenner, 1991; Sweet, 1994). Sweet (1975) reported a more than 10- fold variation in cone production across open-grown *Pinus radiata* stands in New Zealand. Greenwood (1987) reported that the five active seed orchards owned by the Weyerhaeuser Company in the United States of America, scattered throughout a large geographical range, showed a large variation in seed production due to site effects.

The selection of a suitable seed orchard site is *very* complex, especially when there is only a broad understanding of what mix of environmental and edaphic factors are optimal for flowering of the species concerned. This is particularly so because the environmental requirements for strobilus initiation may not be those which are optimal for subsequent cone and seed development.

There are several published references outlining what are generally perceived to be criteria for a "good" seed orchard site (Gallegos, 1978; Zobel and Talbert, 1984; Enescu, 1987). It is generally acknowledged, however, that the difficulty in site selection may be further compounded by micro-environmental effects.

It appears that one of the main criteria of a good site is that it enjoys warm dry summers for optimal strobilus initiation/differentiation (Eriksson, 1982; Griffin, Crane and Cromer, 1984; Owens, Philipson and Harrison, 1992). Further, those conditions may also favour ontogenetically early flowering. Although not well-established, there is widely perceived to be a link between abundant flowering and early flowering. Obviously such early flowering has economic implications for an orchardist (Chapter 1; Sweet, 1994).

It is recognised that good cone-producing sites are frequently close to the coast. This was initially noted for the native stands of *Pinus radiata* (Prof. W.J. Libby, pers. comm.) but has subsequently been reported quite extensively (e.g., Somerville and Sweet, 1978; Carson, 1983).

Fertility of the soil at a site is considered to be an issue in seed orchards. It has been suggested that the soil should not be too fertile nor have too high a water-holding capacity (Zobel and Talbert, 1984). Soils which are very fertile can promote excessive vegetative growth. In their absence, flowering can be partially manipulated by irrigation and fertiliser application (Griffin, Crane and Cromer, 1984); but very fertile, moist sites do not leave an orchardist the management options that are available on a less fertile site.

Although good air drainage is considered beneficial at a site, exposure to excessive winds can be detrimental. Strong winds in seed orchards have been known to cause damage to ramets (Dyson and Freeman, 1968) and particularly strobili, by branch whipping (S. F. Van Ballekom, pers. comm.). The use of shelter of course is an option.

Along with site effects, the genetic material used in a seed orchard can affect the ontogenetic earliness of coning and the overall productivity (Zobel and Talbert, 1984). The variability between clones in their ability to produce strobili has been well documented (e.g., Sweet, 1975; Nikkanen and Velling, 1987). And generally tree breeding programmes do not select for fecundity. Further, the age of the material used to establish the seed orchard will influence the earliness of coning (Zobel and Talbert, 1984).

Apart from environmental and edaphic considerations, other management and social-based issues need to be taken into account when selecting seed orchard sites. Zobel and Talbert (1984) have compiled a list of these.

Gallegos (1978) published a model for selecting the best sites for *Pinus taeda* seed orchards. This model was complex, comprising most climatic factors, together with the well known Thornthwaite soil water balance model. However, from an orchardist view point the ideal tool for predicting possible sites should be one that incorporates easily- interpreted climatic data (Enescu, 1987). There are few examples of such tools reported in the literature.

G. REALISABLE SEED YIELD - AND THE IMPACT OF POST-ANTHESIS LOSSES

The literature clearly accepts flowering or strobilus production as simply the first component of the seed development process. Numerous references are made to the various stages of conifer seed development where large post-anthesis losses due to physiological and environmental factors can occur (see e.g., Matthews, 1963; Sweet, 1975; Lee, 1979; Fenner, 1985; Owens and Blake, 1985; Sedgley and Griffin, 1989). Nonetheless, it is well accepted that obtaining a heavy crop of strobili at anthesis is the first step towards obtaining high potential seed yields from an orchard or forest (Allen and Platt 1990).

CHAPTER 3

STROBILUS PRODUCTION ALONG THE CANTERBURY TRANSECT

A. INTRODUCTION

On the basis of existing knowledge (e.g., Sweet, 1977), Canterbury represents one of the better strobilus-producing areas of New Zealand. But this knowledge is largely based on some 30 years experience with Amberley seed orchard. Information on variability in the production of strobili within Canterbury is quite limited, although knowledge of Canterbury's climatic variability is well documented (Maunder, 1983).

As a prelude to a major study of the impact of site on strobilus initiation, Canterbury seemed to offer a good opportunity for a preliminary study. Amberley, which is within 1 km of the coast is a good strobilus-producing area, while observation suggested that very few strobili were carried on plantations in the mountain areas. Thus a transect running along a latitudinal line from the coast to the foothills might show variability in strobili which could be related to climate.

If such a relationship could be established, it would be beneficial in designing a more substantial survey, in due course. And irrespective of whether a relationship with climate could be established, a pilot study would enable sampling methodology to be designed and tested, and would allow a broadening of knowledge of the timing of long shoot initiation and strobilus differentiation across a range of sites.

At the beginning of this study knowledge on the time when environmental factors were likely to impact on seed-cone differentiation came from bud morphogenesis studies reported by Bollmann and Sweet (1976; 1979), and experiences with $GA_{4/7}$ applications in New Zealand seed orchards.

Bollmann and Sweet (1976; 1979) established for a number of clones in the central North Island that long shoot buds were initiated in mid to late-December and seed-cone buds were recognisable some 6 weeks later.

Experiences with the use of $GA_{4/7}$ applications in seed orchards established that February was generally the month when gibberellin application most increased the numbers of long-shoot primordia that differentiated into seed-cone buds. However, during the time of carrying out this study and developing the model in Chapter 4 more detailed studies on $GA_{4/7}$ application times were made by Siregar (1994). The relevance of those findings to this thesis will be discussed later in Chapter 7.

The intent of the research reported in this chapter was to initiate a preliminary analysis of the variability of strobilus number with site, and its relationship with climate. Because Amberley seed orchard was close to the planned transect, and had an automated weather station, thought was also given as to how it might be used. As a clonal orchard, it could not be compared directly to plantations of seedling origin, and thus could not be a part of the transect. But what did eventuate, was the observation of a considerable variation in the number of strobili produced in the orchard, between the years 1992 and 1993. The relationship of that variation to the weather in the 2 years was analysed, and is presented in this chapter.

B. A PRELIMINARY STUDY TO DETERMINE SAMPLING METHODOLOGY

Several issues were relevant in determining a sampling methodology to count emerging strobili in a comparable manner across a range of sites.

The number of strobili in the crown of a tree is likely to be dependent on the size, and thus in part on the age, of the tree; as well as the aspect, topography and spacing of the stand in which it is growing, and the origin of the seed from which it was established.

There were clearly substantial issues involved in finding stands that were exactly comparable in all these features across the South Island, and thus the key issue in sampling lay in reducing their significance. Firstly it was decided that only forest stands, as distinct from shelterbelts would be sampled. Generally, shelterbelts in the South Island are mechanically trimmed at least once a year so as to encourage branch growth close to the ground, and thus as can be appreciated this practice impacts greatly on the number of strobili carried by shelter trees. A general stand age of between 10 and 12 years was then selected, as stands of that age would all have strobilus-bearing potential. They would probably also have a comparable genetic origin, having been established with open-pollinated seed. And most importantly, a pre-survey

indicated that stands in that age grouping were well represented across the South Island.

To resolve the impact on strobilus number of the variability in tree size with age and site, it was determined that only the emergent strobili in the open-grown top 2 metres of crown would be counted. It was anticipated that, within the narrow age-class structure sampled, the number of strobili in the top of the tree would be relatively independent of tree size; and to some extent independent of spacing and aspect.

To further minimise the impact of topography, aspect and spacing, sampling was restricted to trees on the northern edge of stands growing on relatively flat land.

The remaining issue related to sampling intensity. How many trees per site was necessary to sample to adequately characterise the strobilus-bearing potential of the site?

Preliminary studies on sample size requirements was undertaken in 3, 10-year-old stands at Darfield, Spencerville and Amberley; using the statistical methodology of selecting sample size using confidence limit bounds as means of determining accuracy of estimates (Harraway, 1992). The data indicated that to be able to differentiate at the 95% level of probability between sites differing in mean strobilus counts by 5 per tree, a minimum of 21 trees per site should be sampled. Because the 3 sites examined may not necessarily represent the variability across all sites, and to ensure that sampling error was minimised, it was decided that 40 trees would be sampled in the survey reported here and in Chapter 4.

Preliminary sampling to examine the effect of spacing was carried out at Balmoral Forest. There, strobilus numbers were compared on 10-year-old stands at respectively 1000 and 2000 stems ha^{-1}. The effect of stand age was examined at Waimate, where 10 and 12 year-old stands on adjacent sites were compared. These preliminary studies confirmed that the proposed sampling system was not significantly affected by stand age or spacing, within the limits examined. The transect study was thus proceeded with.

B. MATERIALS AND METHODS

1. Site Locations

Five sites were selected along a gradient running from the coast to the Canterbury foothills along latitude 43°29'S. (refer Table 3.1; Figure 3.1). Each site represented a stand of *Pinus radiata* that was approximately 10 years in age.

Table 3.1

Site location and altitude

Site	Latitude	Longitude	Altitude (m)
Spencerville	43°29'S	172°43'E	4.0
McLeans	43°29'S	172°26'E	70.0
Darfield	43°29'S	172°08'E	190.0
Homebush	43°29'S	172°00'E	220.0
Low Mount	43°29'S	171°30'E	630.0
Amberley	43°10'S	172°20'E	28.0

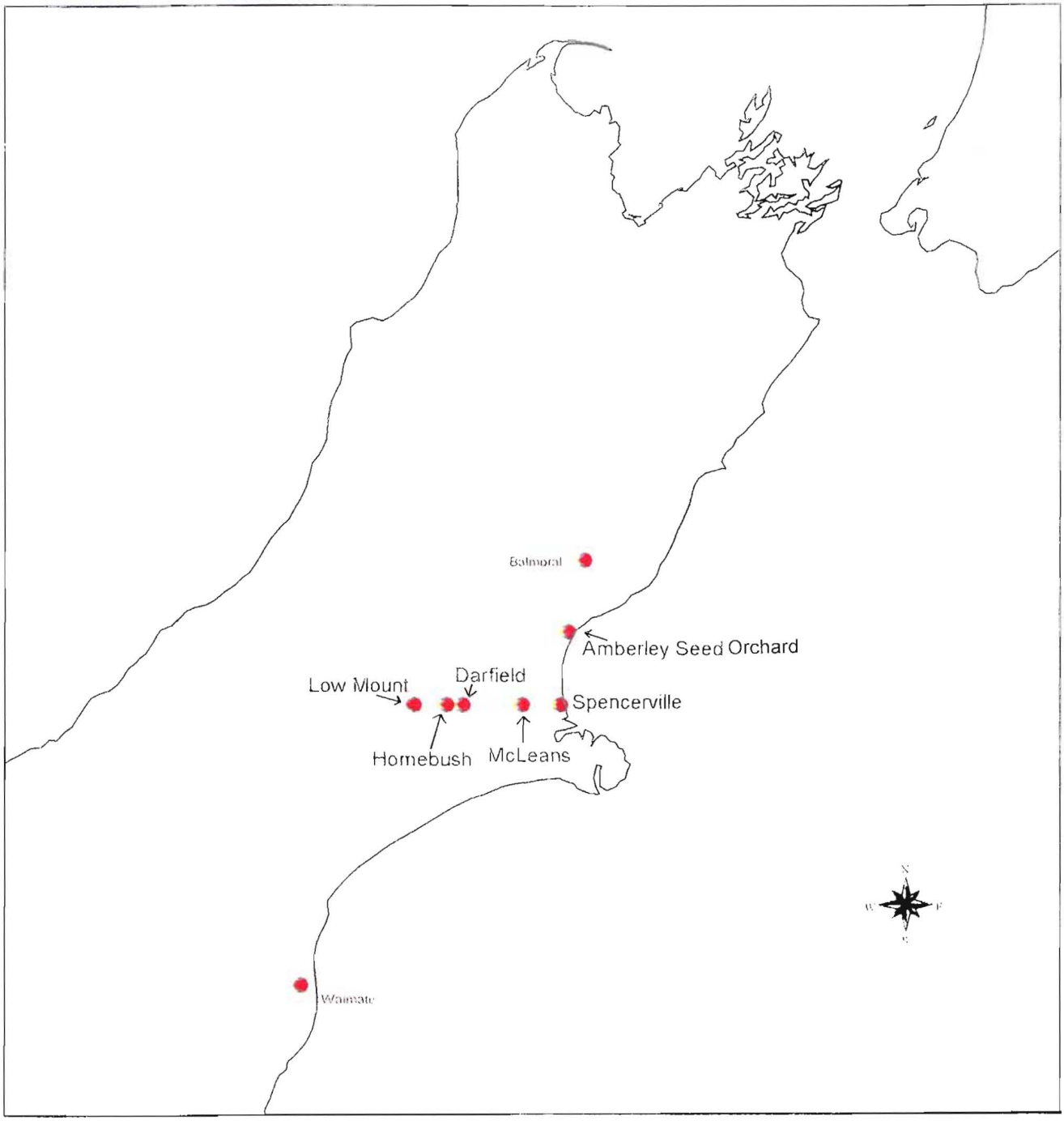

Figure 3.1

A map illustrating the location of the sites on the transect line, relative to Amberley seed orchard. The sites at Balmoral Forest and Waimate where the two pilot studies tested age and spacing effects on the sampling methodology are also shown.

As indicated, Amberley seed orchard, while not one of the transect sites, is located just north of the transect line. Its weather station is a Monitor Sensor Automatic Weather Station (manufactured by Monitor Sensors Pty, Carboolture, Queensland, Australia), and it is configured to collect the following data:

1. Air temperature (daily minimum, daily maximum).
2. Relative humidity (daily minimum, daily maximum).
3. Total rainfall.
4. Total incident solar radiation.
5. Wind speed.
6. Wind direction.
7. Soil moisture.
8. Soil temperature.

2. Climate Measurements

At each site along the transect, temporary weather stations were erected (see Plate 3.1). These stations (Campbell CR10 data loggers) continuously recorded air temperature, soil temperature, photosynthetically active radiation (PAR) and relative humidity, from the beginning of February 1992 to the end of March 1992; a period which was expected to encompass the time of seed cone bud differentiation.

3. Accumulated Growing Degree Days

To relate strobilus development to air temperature, the concept of thermal time was used (Monteith, 1981). This is measured in terms of accumulated growing degree days, GDD, expressed when:

$T_j > T_b$ as

$$GDD = \sum_{j=1}^{n} (T_j - T_b),$$

where T_j is the mean temperature on day j, T_b is the base temperature and n is the number of days during the period of interest. The value GDD (°C day) was a summation of growing degree days over February 1992 and March 1992 at each site on the transect. The base temperature used was 10°C.

4. Soil Water Measurements

Along with the climatological measurements, the root-zone water potential of soils at each site was measured. This was done by Time Domain Reflectometry (TDR - "Trase" System 1) to a depth of 0.3m. The measurements were made on a weekly basis starting on the 22nd of February 1992 and running through to the 28th of March 1992. At each site 3 sets of probes were inserted into the ground equidistant between 4 trees in the outer two rows of the north facing edge of the stand. In total, 3 water potential measurements were made per week at each site.

Samples of the soil at each site were taken from the same area of the stand where the TDR probes were inserted. The bulk density, and wilting point and field capacity values were determined for each sample. The gravimetric wilting point was determined at the Soil Science Department. Lincoln University using a pressure plate and pressure membrane apparatus at -1.5 MPa pressure. Field capacity was determined using a tension table apparatus applying 0.01 MPa suction. By multiplying with the bulk density, the gravimetric values (w/w) were converted to volumetric ones (cm^3cm^{-3}).

Each volumetric reading from the TDR was then converted to a water potential measurement using the root zone matric potential formula (refer Appendix B).

To explore the relationship between seed-cone-bud differentiation and soil-water stress, the parameter water stress integral (S_ψ) was calculated. This is a method of integrating the effect of soil water stress on plant growth and development over time (Myers, 1988). This was calculated as:

$$S_\psi = \sum_{e=1}^{n} (\psi_e),$$

where ψ_e is the mean soil water potential for each weekly measurement (e), and n is the number of weeks during the period of interest.

5. Plant Water Potential

On one occasion during March 1992 at each site, pressure bomb measurements were made on needles. This was done to confirm that root zone soil water potential measurements related to the water potential of the trees, across sites. The technique used was a pressure bomb, or Scholander pressure chamber system (Turner, 1988).

At each site, needles were sampled from branches cut from the top 2 metres of 5 different trees. In total the water potential of 2 needles per tree (each from a different branch) was measured using the needle pressure bomb apparatus described by Gifford (1971). All measurements were made at around 12 noon on a sunny day.

6. Long Shoot Bud Dissections

On 12th of March 1992, bud samples were collected from trees on the transect. The purpose was to confirm that: firstly, February was the time when long shoot bud initiation was occurring in the first annual shoot cycle, and hence an appropriate time to be recording climatological data; and secondly, to examine variability over the transect in the timing of this event.

From five different trees at each site a terminal bud was harvested from a branch that had produced strobili the year before; i.e., was carrying 1-year-old conelets. Following collection the buds were placed in FAA for 24 hrs under vacuum and then moved to a 70% ethanol solution. Buds were then dissected under a dissecting microscope and the number of long shoots in the first-cycle long -shoot region were determined. Buds were identified as either being reproductive or vegetative.

7. Counts of Emergent Strobili

During October 1992 total counts of emerged strobili were made at each site on the transect. Strobili were counted in the top two metres of crown of 40 individual trees. The trees sampled at each site were on the north-facing edge of the stand, and the counts were made from the ground using binoculars. The 2-metre distance was measured using a "Suunto" clinometer. An example of the view of strobili from the ground can be seen in Plate 3.2.

8. Terminology Used to Describe Counts of Current Year's Strobili on Open-Grown Stands

For simplicity in describing and referring to the data on emergent strobili in Chapters 3, 4, 5 and 6 the following terms will be used :

(i) ***"number of emergent strobili"*** - is the mean count per tree of the total current season's strobili in the top 2 metres of crown of 40 trees per site.

(ii) ***"number of first cycle emergent strobili "*** - is the mean count per tree of the total first-cycle current season's strobili in the top 2 metres of crown of 40 trees per site.

9. Amberley Seed Orchard

The counts of mean numbers of emergent strobili per ramet in the orchard were recorded by the orchard staff. The data presented in this chapter (Table 3.5) are means of between 4,000 and 11,000 ramets per clone x 30 clones. The meteorological data collection also was the responsibility of orchard staff.

Plate 3.1

A temporary climate station comprising a louvered Stevenson screen 1.5m above the ground (as per the guidelines of the World Meteorological Organization). A Campbell data logger and temperature/RH sensor can be seen sitting inside the screen. The quantum sensor sat on the top of the screen, while a deep cycle 12 volt battery positioned on the ground below powered the logger. In total 5 of these stations were constructed. Data was down-loaded by a laptop computer. This photograph was taken at Low Mount Forest, Canterbury.

Plate 3.2

A view of a 2 metre region of crown in a 10-year-old tree in which the total number of emergent strobili were counted from the ground using binoculars. This photograph was taken at Rabbit Island, Nelson in 1992 using a 200mm tele-photo lense from the position on the ground from which strobili were counted. The whorls of female strobili can be seen protruding outwards from the newly extended shoots above the green needle mass of the crown .

C. RESULTS

1. Environmental Conditions and Strobilus Counts Across Sites on the Transect

These data are presented in Table 3.2.

The data indicate a reducing gradient in mean temperature, PAR and GDD with increasing distance in from the coast. The only site which did not fit the pattern exactly was Spencerville. A prevailing off-sea breeze tends to lower temperatures slightly, close to the coast.

The water stress integral did not follow the same pattern: it was greatest in the dry inland parts of the plains, reducing both at the coast and in the mountains.

The number of emergent strobili differed significantly across sites, being in particular much higher at McLeans than at any of the other sites. The pattern of strobilus counts across the transect cannot be matched particularly closely with either temperature or soil moisture variability. But there was a tendency for fewer strobili to be produced on cooler sites.

Table 3.3 shows a broad correlation between root zone water potential and plant water potential. On all sites, the needles were more water stressed than the soil. In the coastal and the mountain areas, however, the difference was less than in the drier in-between sites.

2. Shoot Components

These results are presented in Table 3.4

The number of seed-cone primordia differed significantly between sites in a manner that closely parallelled the counts of emergent strobili. McLeans had significantly the highest number, with Low Mount having none.

The production of total long shoot primordia also differed significantly along the transect. The data in Table 3.4 indicate that the high altitude site at Low Mount produced very few long shoots, none of which were seed cones. However, the long-shoot buds at Low Mount were less advanced in their development than those at the lower-altitude sites, and it is possible that at a

later harvest date, more long shoots would have been present.

The number of branch bud primordia did not differ proportionately as much as did seed cone primordia. The parameter which perhaps best matched the climatic changes in the transect was that expressing the number of seed cone initials as a percentage of total long shoot initials. That number decreased from the coast inland.

3. Amberley Seed Orchard - Climatic Conditions and Numbers of Emergent Strobili

These data are presented in Table 3.5 and Table 3.6.

Table 3.5 based on information collected by the seed orchard's management, indicates that, independently of ramet age, 1993 was a very much better year for strobilus production than 1992.

The meteorological data presented in Table 3.6 cover the dates from first cycle long-shoot initiation (in January/February), through the time of strobilus differentiation (in late-February/March) to the time just prior to anthesis which was in July/August.

1992 (the year of lesser strobilus emergence) was in fact warmer than 1993 during February and March. However, in April, May and June, temperatures and growing degree days were substantially warmer in 1993 than in 1992, raising the possibility that the weather at that time may have affected strobilus production.

Table 3.2

Mean site and environmental measurements recorded during February 1992 and March 1992. The emergent strobili were counted at anthesis in October 1992. Emergent strobili data are presented as mean values±SE.

Site (1992)	Air temperature (°C)			Soil temp (°C)	S_ψ (MPa)	PAR ($Wm^{-2}d^{-1}$)	RH (%)	GDD (°C day)	No of Emergent strobili
	min.	mean	max.						
Spencerville	8.1	14.1	20.3	15.9	-4.8	222	80.4	214	6.4±0.91
McLeans	8.7	14.1	20.5	17.3	-8.3	236	78.4	226	19.7±2.62
Darfield	7.5	13.8	21.6	15.9	-8.8	234	75.3	219	4.6±0.93
Homebush	5.8	12.9	21.7	14.8	-7.7	213	74.8	180	5.0±0.82
Low Mount	6.7	11.4	17.5	14.8	-5.5	222	75.2	123	0.0±0.00

Table 3.3

The relationship between soil water potential and needle water potential across the transect sites; all measurements were made at around midday.

Site (1992)	Date of measurement	Root zone water potential (MPa)	Plant water potential (MPa)
Spencerville	14 March	-1.5	-2.1
McLeans	13 March	-1.5	-2.4
Darfield	21 March	-1.5	-2.5
Homebush	16 March	-1.5	-2.4
Low Mount	15 March	-0.8	-0.9
Amberley Seed Orchard	20 March	-1.1	-1.6

Table 3.4

Number of long shoot primordia dissected terminal branch buds collected on 12th of March 1992. Data are presented as mean values±SE.

Site (1992)	Branch primordia	Seed cone primordia	Total long shoot primordia	Seed cones as % long shoot primordia
Spencerville	3.0±0.3	2.6±0.5	5.6±0.3	46
McLeans	5.0±0.8	4.3±0.8	9.3±0.5	46
Darfield	5.3±0.3	1.3±0.7	6.6±0.8	20
Homebush	3.6±0.3	1.3±1.3	4.9±1.5	26
Low Mount	0.6±0.6	0.0±0.0	0.6±0.6	0

Table 3.5

Number of emergent strobili per ramet in the meadow and conventional hedge orchard at Amberley seed orchard. Ramets were from a range of representative clones with regard to levels of strobilus production in the orchard. Data are presented as mean values across clones.

Orchard type	Age class (years after planting)	Numbers of emergent strobili	
		1992	1993
Meadow	2	2.7	3.9
	3	4.9	9.5
Conventional hedge	5	14.8	17.2

Table 3.6

Temperature and light measurements recorded for the first six months of each of the years 1992 and 1993 at Amberley seed orchard.

Year	Month	Temperature			GDD (°C days)	Solar radiation (MJ $m^{-2}d^{-1}$)
		min	mean	max		
1992						
	January	10.5	15.4	21.0	119.9	22.6
	February	10.0	15.4	22.0	158.1	18.3
	March	8.0	13.5	20.0	112.5	14.9
	April	4.4	9.5	14.9	15.5	9.7
	May	2.4	7.0	12.1	7.4	6.1
	June	1.2	5.4	9.9	3.3	4.7
1993						
	January	9.7	15.5	21.0	156.7	18.3
	February	10.5	14.6	19.0	121.1	16.7
	March	7.3	12.8	18.1	91.3	12.9
	April	6.2	10.9	15.7	54.6	8.8
	May	3.5	9.2	14.5	22.2	5.7
	June	4.0	9.8	13.9	33.8	4.6

D. DISCUSSION

This study was a preliminary one to develop a sampling method; to obtain information on the variability in numbers of emergent strobili in *Pinus radiata* along a climatic gradient; and to relate the variability to climate.

The procedure of counting strobili in the top 2 metres of crown from the ground, with binoculars, proved to be a feasible one. The average time taken to do this for 40 trees was 2.5 hours. Working from the north side of a stand margin gave good lighting conditions: the operator was comfortable that counting errors (due to strobili not being visible) were not excessive, and were comparable between sites. That is, although the counts from the ground may not have been absolute in their accuracy, the relative ranking of the sites for strobilus production was generally accurate.

Across the 5 sites on that transect, with mean numbers of strobili per tree ranging from 0 to 19.6, the standard deviation did not exceed 20% of the mean at any site.

The numbers of emergent strobili varied substantially and significantly between study sites. With only five sites in the transect, no attempt was made to explore the relationship with February/ March weather in a statistical manner. But certainly the results were not clear-cut. The most productive site in terms of numbers of strobili was McLeans, which was neither the warmest nor the driest site. But it was the site with the highest number of GDD's. It also had (just) the highest amount of photosynthetically active radiation.

The lack of a good relationship between strobilus numbers and temperature and soil moisture in February and March, a period shown (by bud dissection) to encompass the time of strobilus differentiation at all sites except possibly Low Mount, must be taken as an indication **either** that temperature and soil moisture are not the key climatic variables affecting strobilus differentiation, **or** that other factors may also be important.

More useful information on the relationship of weather to numbers of strobili came from the meteorological data collected at Amberley seed orchard. Based on that information, temperature and GDD during the months of April, May and June, **after** first cycle strobili have been differentiated, may be important in determining emergent strobilus numbers. Those

meteorological data of course were not collected on the transect.

Based on the literature, it is not difficult to accept that potential strobilus numbers can be affected by weather conditions following their differentiation. The work of Silen (1973a) in particular has demonstrated clearly that the ultimate direction of a differentiating long-shoot can be modified over quite long periods of time after its initial differentiation. It can be postulated at Amberley that there was a "loss" during the winter months of potential strobili; and that this loss was higher in a cold winter than in a mild one. If that interpretation is correct, it will clearly make modelling of the impact of site on strobilus initiation more complex than if only the weather at the time of strobilus differentiation was important.

CHAPTER 4

DEVELOPMENT OF A STATISTICAL MODEL TO PREDICT NUMBERS OF NEWLY EMERGED FEMALE STROBILI

A. INTRODUCTION.

With increasing demand for genetically improved *Pinus radiata* seed (Vincent, 1993) it is envisaged that new seed orchard sites are going to be required in New Zealand (Chapter 1). In Chapter 3, a preliminary exploration was made of variability in numbers of strobili with site. In this chapter, a much more detailed study is described, which had as its objective the development of a statistical multivariate model to predict numbers of newly emerged strobili across a range of sites in New Zealand.

The issue as to why numbers of newly emerged strobili were chosen for analysis, in contrast for example to numbers of mature cones, needs some explanation. Obviously, with regard to seed orchard siting, the factor of interest to be optimised is total seed yield per hectare. And strobilus emergence at anthesis is simply the first contributing component of this. Essentially, it was decided that as much information as possible was required regarding the individual components of seed production. Thus the study reported in this chapter in fact assessed not only numbers of newly-emerged strobili, but also the incidence of subsequent abortion. Mature cones were also harvetsed to assess numbers of full seeds per cone, and seed weights.

In this chapter, numbers of strobili will be reported and modelled. In Chapter 6, those data will be expanded to include the other parameters assessed.

An early issue requiring decision was the area from which data on strobilus production would be collected. It was decided to restrict this to that part of the South Island east of the Southern Alps for the following reasons:

(a) That area was believed to include both some of the most productive and least productive strobilus-bearing sites in New Zealand.
(b) In climatic terms it offered temperature variability which was relatively simple; thus offering the prospect of developing reasonable statistical relationships.
(c) It was a workable area in terms of costs and logistics.

One of the difficulties of developing statistical relationships involving climate and soil variables is the high level of interdependence that exists between them. However, various techniques of multivariate analysis can be used to perform such a task.

Multivariate analysis is a mathematical technique that can measure, explain and/or predict the degree of relationship among variates; for example, biological and environmental variables, respectively (Manley, 1992). The most appropriate technique to use depends on the number of variables involved , their levels of dependence, whether the data are metric or non-metric, etc. A good analysis of these issues is given by (Hair *et al.*, 1979). Based on that consideration, multiple regression analysis (which is appropriate for a dependence method, with dependent variables and all metric data) emerged as the most appropriate tool to use in this study. For *Pinus radiata,* multiple regression and principle component analysis, have both been used previously to predict site index across a range of climates in New Zealand (Jackson and Gifford, 1974; Hunter and Gibson, 1984). Generally, these models comprised interdependent climatic and soil variables; and accounted for around 50% or 60% of between-site variability of the dependent variable (site index). Similarly, for *Nothofagus solandri* (Fagaceae), Allan and Platt (1990) used multiple regression analysis to account for the variability in seed production between sites in the Canterbury (New Zealand) high country.

An initial issue in this study was the selection of appropriate environmental variables for the multiple regression analysis. It was known from the literature that temperature and soil water status were likely to play a key role in the outcome of seed-cone bud differentiation.

At the time of beginning to model strobilus numbers, knowledge on the timing when environmental factors were likely to first impact on seed-cone bud differentiation came from the published findings on bud morphogenesis by Bollmann and Sweet (1976; 1979). Based on those references it was considered that February was the time when temperature, for example, was most likely to impact on the number of strobilus buds that begin differentiating. The bud dissection results in Chapter 3 confirmed that around this time seed-cone buds were beginning to form.

The intent of the study reported in this chapter was to develop a multiple regression model for predicting numbers of emergent female strobili of *Pinus radiata* across a range of sites and climates.

B. MATERIALS AND METHODS

1. Site Selection

Fifty two sites (coastal and inland) growing stands of *Pinus radiata* between the ages of 10 and 12 years old were selected along the east side of the main dividing range of the South Island of New Zealand. All sites were selected within 10 kilometres of climatological stations recording daily temperature and rainfall measurements; these data were required for the multiple regression analysis. Five of the 52 sites were previously used on the Canterbury transect and reported in Chapter 3.

The sites chosen are listed in Table 4.1 and are mapped in Figure 4.1. The sites ranged in latitude from 41°10'S to 45°59'S and in altitude from 4m to 630m above sea level.

Table 4.1

Location and height above sea level of the 52 sites. The sites are listed in descending order according to strobilus counts.

No	Site (1992)	Latitude	Longitude	Altitude (m)
1	Rabbit Island	41°16'S	173°08'E	4.0
2	Motueka	41°10'S	173°01'E	121.0
3	Appleby	41°13'S	173°02'E	117.0
4	Grassmere	41°41'S	174°08'E	40.0
5	Kaikoura	42°25'S	173°40'E	2.0
6	McLeans	43°29'S	172°26'E	70.0
7	North Bank	41°26'S	173°42'E	200.0
8	Makikihi	44°25'S	171°07'E	8.0
9	Mayfield	43°46'S	171°23'E	320.0
10	Birch Hill	41°39'S	173°16'E	300.0
11	Ashley Forest	43°14'S	172°37'E	214.0
12	Blenheim	41°33'S	173°65'E	20.0
13	Woodend	43°20'S	172°40'E	4.0
14	Moeraki Boulders	45°21'S	170°50'E	40.0
15	Waimate-10	44°44'S	171°04'E	40.0
16	Salt Water Creek	43°16'S	172°43'E	5.0
17	Rakaia	43°43'S	172°04'E	110.0
18	Awatere Valley	41°43'S	173°54'E	200.0
19	Spotswood	42°45'S	173°14'E	60.0
20	Oamaru	45°05'S	170°49'E	30.0
21	Wairau Valley	41°34'S	173°32'E	160.0
22	Rangitata	44°11'S	171°30'E	4.0
23	Waimate-12	44°44'S	171°04'E	40.0
24	Argyle	41°41'S	173°12'E	400.0
25	Winchmore	43°45'S	171°48'E	170.0
26	Lincoln	43°37'S	172°22'E	40.0

27	Rangiora Nursery	43°00'S	172°33'E	15.0
28	Kurow	44°46'S	170°31'E	198.0
29	Spencerville	43°29'S	172°43'E	4.0
30	Lake Waihola	45°59'S	170°06'E	32.0
31	Merivale Station	44°44'S	169°31'E	400.0
32	Orari	44°08'S	171°16'E	80.0
33	Amberley Beach	43°10'S	172°21'E	3.0
34	Homebush	43°29'S	172°00'E	220.0
35	Amberley	43°10'S	172°20'E	28.0
36	Tapanui	45°56'S	169°17'E	250.0
37	Darfield	43°29'S	172°08'E	190.0
38	Cromwell	45°03'S	169°11'E	200.0
39	Balmoral	42°49'S	172°51'E	160.0
40	Eyrewell-Wrights	43°24'S	172°11'E	210.0
41	Burkes Pass	44°05'S	170°39'E	500.0
42	Wanaka	44°40'S	169°11'E	300.0
43	Hanmer	42°32'S	172°52'E	387.0
44	Eyrewell-Downs	43°26'S	172°22'E	110.0
45	Dunsandel	43°35'S	171°59'E	158.0
46	Crown Range	45°58'S	168°53'E	600.0
47	Dunback	45°30'S	170°31'E	540.0
48	Dunedin	45°53'S	169°58'E	432.0
49	Tara Hills	44°30'S	169°55'E	488.0
50	Glynn Wye	42°36'S	172°28'E	600.0
51	Hororata-West	43°31'S	171°50'E	306.0
52	Low Mount	43°29'S	171°30'E	630.0

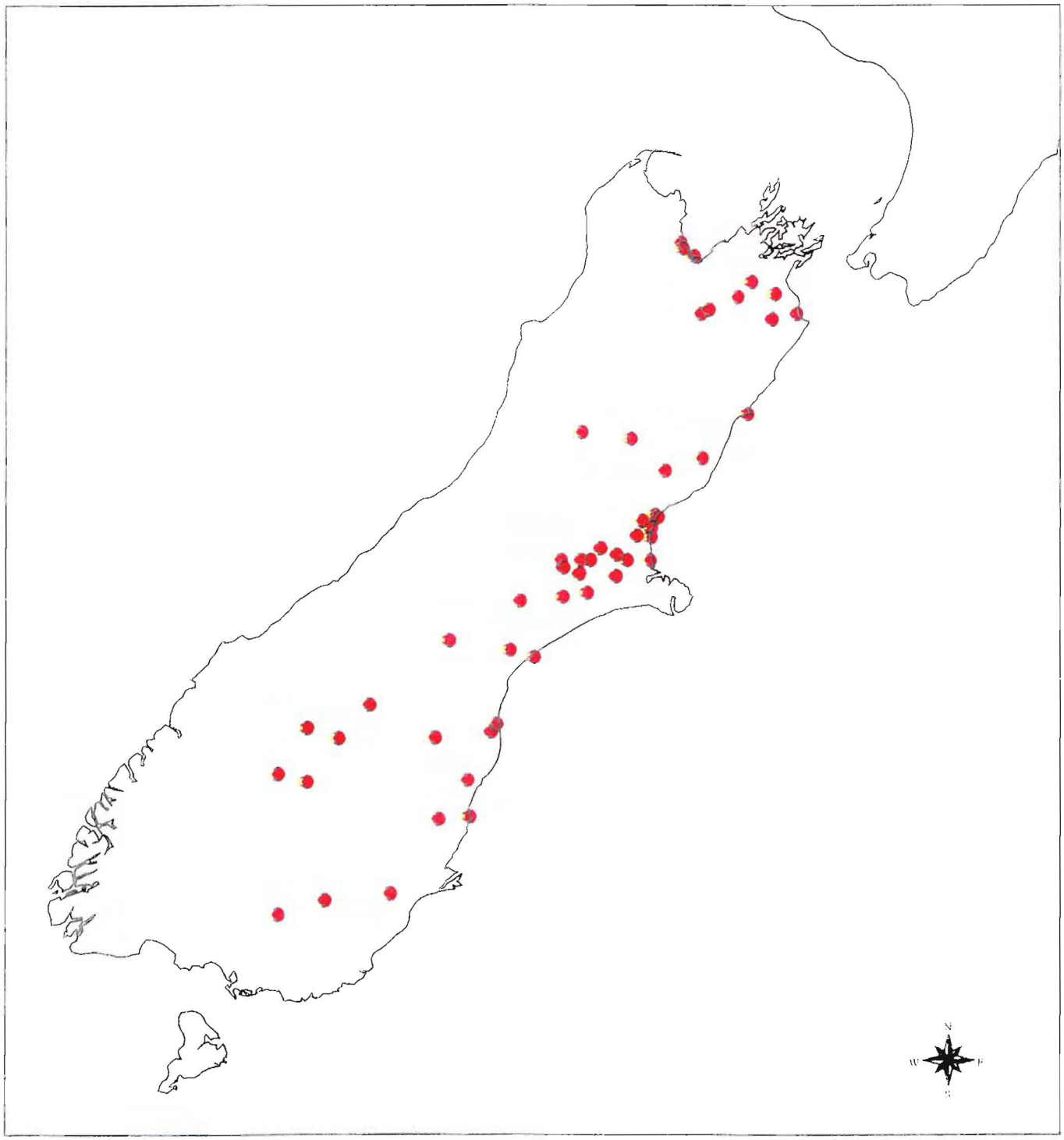

Figure 4.1

A map of the South Island illustrating the location of sites at which strobilus counts were made in 1992.

2. Counts of Strobili

During October 1992, counts of emergent strobili were made (as described in Chapter 3). Strobili were counted in the top two metres of crown of 40 trees at each site. A full account of the methodology is given in the Materials and Methods section in Chapter 3.

3. Other Tree Parameters

At the time counts of emergent strobili were being made other parameters of tree growth that were considered to be possibly related to strobilus number were made. Similarly, cones were collected from each site in order to obtain data on seed yield. These data are presented, analysed and discussed later in Chapter 6.

4. Climatological Data

The preliminary exploration of site/strobilus number relationships reported in Chapter 3, suggested that temperature, GDD and soil moisture during the time of long shoot initiation and differentiation, may be significant variables; as may temperature during the autumn and winter months post-initiation and leading up to anthesis. Logic also suggested that the weather in the spring **prior** to long shoot initiation could influence crown growth, and thus the number of potential sites for strobilus initiation. Those, then became the meteorological data sought.

Climatological data recorded during 1991 and 1992 were obtained from the New Zealand National Institute of Water and Atmospheric Research Ltd (N.I.W.A.). Temperature data were corrected for any altitudinal differences between climate station and stand. The adiabatic lapse rate used was 0.34°C per 100m, and 0.40°C per 100m respectively, for sites below and above 300m (Norton, 1985). The maximum altitudinal adjustment made was 410 metres. Rainfall data were not adjusted for altitude, both because of the complexity of this task, and because there were sufficient rainfall recording stations available that the distances and altitude differences between stand sites and recording sites were not excessive.

5. Soil Moisture Model

When strobilus counts were made in October, 1992, soil moisture measurements were not taken. This was because the strobili which were counted had been initiated and developed earlier in the year; and it was the soil moisture at **that** time which would have been relevant to strobilus numbers. Thus, it was necessary retrospectively to obtain data on early 1992 soil moistures at the range of sites used.

A simple forest water balance model (Whitehead and Kelliher, 1991) was used to estimate root zone water potential for all sites at which emergent strobili were counted. A description of the model is given in Appendix B. The inputs for this model were:

(1) Weather data (temperature, rainfall and solar radiation).

(2) Soil water holding capacity.

The model was used as a simple tipping bucket model in the sense that the drainage function was set such that drainage only occurred when the soil reached field capacity (see schematic diagram in Appendix B).

Before using this model, however, it was validated across twenty sites in both the North Island and South Island during February 1994 to ensure its appropriateness (refer to Appendix C).

At each site a pit was dug to 0.4m and a sample of soil taken. The pit was dug equi-distant between four trees in the outermost two rows of the north-facing edge of each stand.

The moisture content of each soil sample was then measured on a gravimetric basis (w/w). Further, for each sample the bulk density, stone volume (>2.5mm) and plant available water content (AWC=FC-WP) (refer to Materials and Methods in Chapter 3) were measured.

Climatic data starting from June 1993 to March 1994 was obtained from N.I.W.A. Unlike temperature and rainfall, solar radiation data were not available for every official recording site. However, it was recorded by at least one in every 6 climate stations. For sites without solar radiation measurement, the values of the nearest recording climate station were used.

For each site the soil water balance model was run from the 1st of June 1993 until 31st of March 1994, starting with the soil water storage at field capacity. The root zone depth was set at 0.4m. The level of root-zone water stress was calculated on a daily basis.

The actual soil water measurements made in February, (i.e., the gravimetric ones) were converted to matric potential (-MPa) and then compared to those predicted by the model. The validation is presented in Appendix C.

Following the validation of the soil water model, the daily root-zone soil-water-potential for the 1992 sites was estimated from June 1st 1991 to March 31st 1992. As for the 1994 validation sites, soil samples were collected from each of those sites to 0.4m and the volumetric water holding capacity of each soil was determined. For each site the daily water potential estimates of the model were integrated over time.

6. Soil Classification

The class, texture, citric phosphate level and pH for the soil at each site was documented. This information was obtained from soil maps and associated information published in: Chittenden, Hodgson and Dodson (1966); New Zealand Soil Bureau Bulletin, 27; and New Zealand Soil Bureau Bulletin, 26.

7. Accumulated Growing Degree Days (GDD)

These calculations relate to the influence of climate on the vegetative growth of the crown, and the consequent implications regarding the number of potential strobilus sites.

For each location, the number of growing degree days (GDD) from the 1st of August 1991 to the 31st of November 1991 was calculated, using the formula described in Chapter 3.

Preliminary investigation using principle component analysis indicated that sites that were either cool and dry, or cool and moist during the spring produced fewer strobili, than sites which were warm and moist. To gain some measure of these effects, parameters were developed in which accumulated growing degree days were weighted firstly against rainfall, and secondly against soil water stress.

8. Accumulated Growing Degree days (G_r) Weighted Against Spring Rainfall (August 1991- November 1991)

This was expressed as;

$$G_r = \sum_{j=1}^{n} T_j - T_b \times \sum_{i=1}^{n} r/m,$$

where T_j is the mean temperature on day j, T_b is the base temperature of 10°C, r is daily rainfall at individual sites on day i and m is the mean rainfall during period n for all 52 sites in the study. The period of interest (n) was from 1st August 1991 to the 31st November 1991.

If on the one hand the rainfall at a site was above the overall average of all the sites in the study, it was regarded as probable that soil water was not limiting for growth, and G_r was multiplied by a value greater than 1. If on the other hand a site had a below- average rainfall then G_r was multiplied by a value less than 1; as the soil was drier, and thus regarded as slowing growth.

9. Accumulated Growing Degree Days (GDD) Weighted Against Spring Soil Water Stress Integral(S_ψ)

This was expressed as;

$$G_{s\psi} = \sum_{j=1}^{n} T_j - T_b \times 1 - (\sum_{s=1}^{n} S_\psi/-180.5),$$

where Tj is the mean temperature on day j, T_b the base temperature of 10°C, S_ψ is the daily soil water potential on day s divided by 180.5; the latter value being the difference between cumulative S_ψ of soil always at field capacity and soil always at wilting point for the 122 days (n) over the spring period; this being from 1st August 1991 to the 31st November 1991.

If soil was at field capacity (-0.02 MPa) for the whole period from August to November, the soil water stress integral for the 122 days would be -2.44 MPa (122× -0.02 MPa), which would mean the $G_{s\psi}$ value would be multiplied by a value close to 1. On the other hand if soil was always at wilting point (-1.5 MPa) the soil water stress integral would be -183 (122*-1.5 MPa) and the $G_{s\psi}$ value would be multiplied by 0; implying that no growth would have occurred.

10. Statistical Analysis

The normality of the strobilus data was tested using the PROC UNIVARIATE procedure (SAS Institute, 1987). It was found that the data were positively skewed and so a $\log_e$- transformation was carried out on the data to satisfy regression assumptions (Finney, 1973).

10.1 Correlation Analysis - Strobilus Counts with Climatic and Soil Variables

The level of agreement between numbers of emergent strobili and monthly temperature (December 1991 - June 1992), soil water stress integral (i.e., for August to November 1991 and February and March 1992) and rainfall variables was measured with the Pearson's correlation coefficient using the PROC CORR procedure (SAS Institute, 1987).

In developing the correlations, the pattern used was initially to work with the variable of temperature which had been shown to be important in Chapter 3. Then, once the significance of temperature at different stages in the development cycle was understood, other variables which logic suggested might be implicated were introduced and tested.

10.2 Stepwise Regression - Strobilus Counts With Climatic and Soil variables

The capacity to predict numbers of emergent strobili (the dependent variable) by any of the variables tested by the correlation analysis was then analysed by stepwise, multiple linear regression using the PROC REG procedure (SAS Institute, 1987). All variables which were significantly correlated with emergent strobilus numbers were included in the multiple regression. Both forward-selection and backward-selection procedures were used to confirm the findings of the step-wise model.

The F statistic was the criterion the model used for selection of independent variables into the equation. The significance level for the F statistic was set at 10%.

10.3 Correlation Analysis Between Soil Type and Strobilus Counts

The level of association between numbers of emergent strobili and soil classes, phosphate and pH data across sites was analysed by correlation analysis. The eight main soil classes in the South Island were assigned a value from 1 to 8. Similarly, the textural classes were also ranked, from 1 to 7. The published data for phosphate and pH were used directly in the analysis.

The soil class scores mean the following:

1 = Brown grey earth.
2 = Yellow grey earth.
3 = High country yellow brown earth.
4 = Upland yellow brown earth.
5 = Intergrade yellow grey earth.
6 = Yellow brown earth.
7 = Recent soil.
8 = Yellow brown sands.

The soil texture scores were as follows:

1 = Sand
2 = Loamy sand
3 = Stoney intergrade between sand and silt.
4 = Sandy loam.
5 = Stoney sandy loam.
6 = Silt loam.
7 = Clay loam.

The soil phosphorous levels were categorised as follows:

>22	Very high
16-22	High
6-12	Medium
2-6	Low
<2	Very low

The level of phosphate in the soil was determined by the 2 % citric soluble phosphate test.

C. RESULTS

1. Strobilus Counts Across Sites

These data are presented in Table 4.2

Across the 52 sites the numbers of emergent strobili in the top 2 metres of crown ranged from 0 to 31.9, with a mean of 9.63±1.26. The differences between sites were highly significant, with the 10 most productive sites carrying an average of 21.84 strobili compared to the overall average of 9.63.

2. Correlation of Temperature with Numbers of Emergent Strobili

Table 4.3 presents correlations between temperatures during a 7-month period prior to anthesis, and the number of strobili counted at anthesis; across the 52 sites.

Overall, minimum temperature was more highly correlated with strobilus number than was mean temperature; and maximum temperature was not well correlated at all. Minimum temperature was in fact correlated with emerging strobilus number at the 0.0001% level during every one of the 7 months. The correlations ranged from 0.59 (January) to 0.74 (February). Temperatures during the 7 months were of course also inter-correlated with one-another. The correlation between the May and February minimum temperatures across all sites was 0.68, and the May temperatures were also highly correlated with those of April and June.

There were 2 periods in which correlations between temperature and strobilus number at anthesis were higher than others: in February, when long shoots were differentiating, and in May when differentiated long shoots were maturing. May and February minimum temperatures have been carried forward to Table 4.4, along with other variables which were tested against emergent strobilus numbers.

Firstly, Table 4.4 shows that neither accumulated growing degree days for February, nor the soil water stress integral for February and March had correlations which were anywhere as near as high as those for February temperature. They were, however, statistically significant, with soil water stress being negatively correlated with strobilus production. That is, sites with a higher

water stress during the time of strobilus differentiation carried more strobili than those with less water stress. Note that the validation of the soil water model (presented in Appendix C) generally predicted root zone water potential to within 0.3 MPa of what was actually measured; although for 2 sites (Rabbit Island and Hanmer) the model was relatively inaccurate.

A number of factors which may influence vegetative growth in the spring prior to strobilus initiation, and thus influence the number of strobilus-bearing sites, were significantly correlated with strobilus number. Accumulated growing degree days from August to November was the component which explained most of the variability (r =0.46); and this relationship was reduced when this variable was weighted against either rainfall (r=0.39) or soil water stress (r=0.32). All 3 variables were in fact inter-correlated.

2. Stepwise Multiple Regression - Number of Emergent Strobili

The results of the stepwise regression analysis are presented in Table 4.5. Data for the independent variables are included in Table 4.6.

All variables that were significantly correlated with emergent strobili, from both Tables 4.3 and 4.4 were included in the multiple regression analysis.

The results indicated that at step one, February minimum temperature explained around 54% of the variability in emergent strobili across sites. At step 2, when accumulated growing degree days for the previous spring (weighted against rainfall) was added, the predictive ability of the model improved to 58%. When the next significant variable February/March soil water stress integral was selected at step 3, the model's coefficient of determination increased another 6% to 64%. Finally, the last variable to be selected, that only improved the model a further 1%, was May minimum temperature; and this variable was only significant at the 10% level. The variables: G_f (GDD for February); $S_{\psi 2}$ (soil water stress integral for the previous spring); GDD (GDD for the previous spring); and $G_{s\psi}$ (GDD weighted against soil water stress integral for the previous spring) were not selected into the model equation.

Regression coefficients together with their standard errors are listed in Table 4.5.

Of the other significantly correlated temperature variables from Table 4.3. Mean May temperature was significant at the 10% level; and was as equally good as mean May minimum temperature as a predictor in the model. The others were not significant; even at the 10% level.

3. Appropriateness of Predictive Model - Plot of Residuals

These are presented in Figure 4.2.

Although statistical significance has indicated the appropriateness of the model equation, this is further supported by the plot of the actual values against the residual values. The residuals appear to be reasonably normally distributed: the mean value of the residuals was 0 and their standard deviation 0.45. Over 70% of the residuals were within 2 deviations, giving reassurance that the model equation is appropriate.

5. Correlations Between Soil Type and Strobilus Counts

Soil data for each site are presented in Table 4.7.

Soil mineral nutrients have in the past been associated with strobilus production. Although it was beyond the scope of this study to measure soil nutrition across all the survey sites it was possible to broadly classify the soil type at each site and obtain some published estimates of soil pH and citric phosphate content.

On the basis of these data there were no strong correlations between strobilus number and soil phosphate level, pH or texture. However, there was a significant correlation between strobilus number and soil class. The counts of strobili recorded on the sites with soils in the yellow brown earths, yellow brown sands and recent soil classes were higher than those on sites with the brown grey earths, yellow grey earths and high country yellow brown earths.

Table 4.2

Mean numbers of emergent strobili across eastern South Island sites. Counts were made in October 1992; on trees aged between 10 and 12 years. At each site the number of strobili in the top 2 metres of crown of 40 trees were counted. The data presented are means per tree.

No	Site sampled in 1992	Mean total number emergent strobili	Standard error
1	Rabbit Island	31.9	3.46
2	Motueka	28.4	2.58
3	Appleby	24.2	3.11
4	Grassmere	20.1	2.17
5	Kaikoura	19.8	1.63
6	McLeans	19.7	2.24
7	North Bank	19.6	1.89
8	Makikihi	19.3	1.86
9	Mayfield	18.5	2.12
10	Birch Hill	16.9	2.25
11	Ashley Forest	16.1	2.03
12	Blenheim	15.0	2.22
13	Woodend	14.6	1.60
14	Moeraki	14.0	1.17
15	Waimate-10	12.6	1.65
16	Salt Water Creek	12.4	1.72
17	Rakaia	11.5	1.29
18	Awatere Valley	11.5	1.49
19	Spotswood	10.3	1.87
20	Oamaru	10.1	1.41
21	Wairau Valley	10.0	1.68
22	Rangitata	10.0	1.37
23	Waimate-12	9.5	1.54
24	Argyle	9.3	1.25
25	Winchmore	9.0	1.08

26	Lincoln	8.3	1.07
27	Rangiora Nursery	7.9	1.18
28	Kurow	6.5	1.06
29	Spencerville	6.4	0.91
30	Lake Waihola	5.9	0.93
31	Merivale Station	5.4	0.71
32	Orari	5.2	0.86
33	Amberley Beach	5.1	1.39
34	Homebush	5.0	0.82
35	Amberley	4.8	0.75
36	Tapanui	4.7	0.87
37	Darfield	4.6	0.94
38	Cromwell	4.5	0.69
39	Balmoral	4.1	0.68
40	Eyrewell - Wrights	3.9	0.56
41	Burkes Pass	3.8	0.85
42	Wanaka	3.7	0.78
43	Hanmer	3.3	0.43
44	Eyrewell - Downs	3.1	0.51
45	Dunsandel	2.9	0.69
46	Crown Range	1.8	0.41
47	Dunback	1.6	0.41
48	Dunedin	1.2	0.42
49	Tara Hills	1.2	0.25
50	Glynn Wye	1.1	0.31
51	Hororata - West	0.9	0.38
52	Low Mount	0.0	0.00
Pr>F (site)		0.0001	
Mean of top 10 sites		21.84	
Mean of 52 sites		9.63	
Range of 52 sites		0 - 31.9	

Table 4.3

Correlations (r) of number of emergent strobili with mean monthly minimum, mean and maximum temperature. Significance levels (Pr>F) are given in parentheses.

Variable month (Year)	Strobili (r)		
	min	mean	max
December (1991)	0.60 (0.0001)	0.39 (0.0038)	0.07 (0.6336)
January (1992)	0.59 (0.0001)	0.42 (0.0018)	0.04 (0.7814)
February (1992)	0.74 (0.0001)	0.50 (0.0001)	0.16 (0.2414)
March (1992)	0.60 (0.0001)	0.46 (0.0005)	0.21 (0.1263)
April (1992)	0.60 (0.0001)	0.63 (0.0001)	0.33 (0.1490)
May (1992)	0.68 (0.0001)	0.72 (0.0001)	0.66 (0.0001)
June (1992)	0.66 (0.0001)	0.70 (0.0001)	0.65 (0.0001)

Table 4.4

Correlations (r) of mean total counts of strobili with site climate and soil variables. Significance levels (Pr>F) are given in parentheses.

Climatic/soil variable	Mean total number of emergent strobili (r)
Summer/autumn conditions (1992)	
Feb	0.74 (0.0001)
G_f	0.37 (0.0058)
S_ψ^1	-0.30 (0.0275)
May	0.68 (0.0001)
Spring conditions (1991)	
Rain	-0.02 (0.8791)
S_ψ^2	-0.26 (0.0513)
GDD	0.46 (0.0004)
G_r	0.39 (0.0033)
$G_{s\psi}$	0.32 (0.021)

The variables have the following meaning:

Feb - mean minimum temperature (°C) for February 1992.

$S_{\psi 1}$ - soil water stress integral for February 1992 and March 1992.

$S_{\psi 2}$ - soil water stress integral for August 1991 and November 1991.

May - mean minimum temperature (°C) for May 1992.

Rain - total rain from August 1991 to November 1991.

G_f - accumulated growing degree days (°C day) for February 1992

GDD - accumulated growing degree days (base 10°C) from August 1991 to November 1991.

G_r - total degree days (base 10°C) from August 1991 to November 1991 weighted against rainfall

$G_{s\psi}$ - total degree days (base 10°C) from August 1991 to November 1991 weighted against the soil water stress integral for those months.

Table 4.5

Table of partial coefficients of determination from stepwise multiple linear regression of log_e-transformed emergent strobili across Eastern South Island sites. Variables are shown in the order of selection by the regression analysis and the overall model coefficient of determination is given following the inclusion of each variable. Significance levels are also given (p values for the F statistics).

Variable	Sums of squares due to regression	Residual mean square	Pr>F	Coefficient of determination (r^2)
Feb temp.	16.98	0.28	0.0094	0.54
G_r	18.13	0.26	0.0044	0.58
S_ψ^1	19.98	0.23	0.0164	0.64
May temp.	20.54	0.22	0.1225	0.65
Total due to regression:	20.54			
Residual sum of squares:	10.74 on 51 df			
Total sum of squares:	31.29			

The four variables listed accounted for around 65% of the overall variation of Y about its mean value. The regression coefficients, together with their standard errors, are listed:

Variable	Coefficient	S.E.
Feb. temp.	0.146	0.053
G_r	0.002	0.001
S_ψ^1	-0.009	0.003
May temp.	0.102	0.063
Intercept term	-0.143	

The corresponding equation may be written as follows:

Log_e(strob) = 0.146 (Feb temp) + 0.002 (G_r) - 0.009 (S_ψ^1) + 0.102 (May temp) - 0.143

The variables have the following meaning:

Log_e(strob) - number of emergent strobili (log_e-transformed to satisfy regression assumptions)

Feb temp. - mean minimum temperature (°C) for February 1992.

G_r - accumulated growing degree days (base 10°C) from August 1991 to November 1991 weighted against rainfall for those months.

S_ψ^1 - soil water stress integral (-MPa) for February 1992 and March 1992.

May temp. - mean minimum temperature (°C) for May 1992.

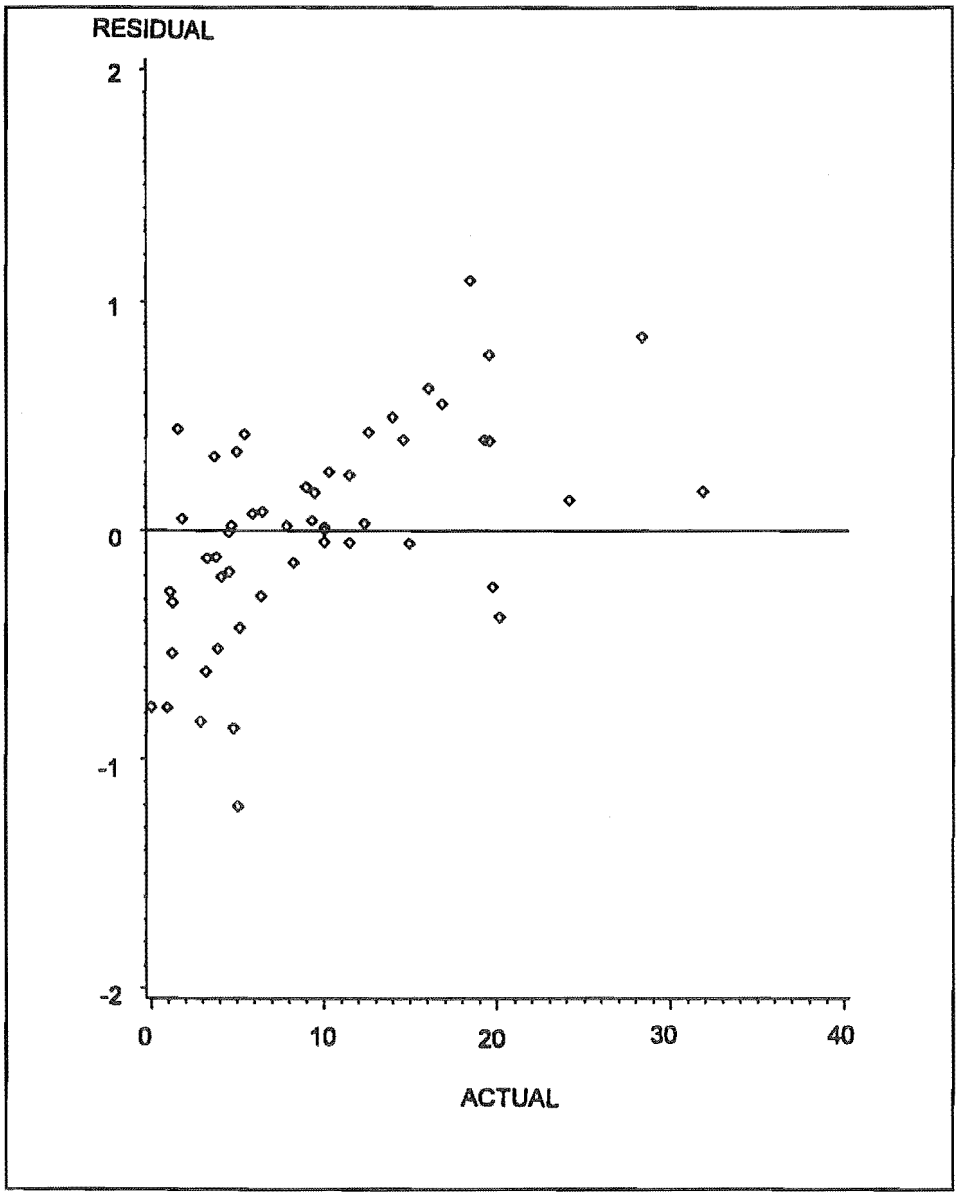

Figure 4.2

A graph of the actual versus residual (actual-predicted) values for the model of the 1992 strobilus counts across the eastern South Island.

Table 4.6

Mean values for the independent variables and counts of strobili for the strobilus production model; data were collected in 1991 and 1992.

No	Site - sampled in 1992	Mean No strobili (1992)	[1]Mean min. Feb. temp. (1992) (°C)	[2]Total Rainfall Aug.-Nov. (1991) (mm)	[3]Soil ψ Feb.-March (1992) (MPa)	[4]GDD Aug.-Nov. (1991) (°C day)	[5]Mean Min May temp. (1992) (°C)
1	Rabbit Island	31.9	11.8	195	-66	279.5	3.0
2	Motueka	28.4	10.0	170	-86	287.7	2.5
3	Appleby	24.2	11.9	191	-84	350.8	2.6
4	Grassmere	20.1	13.7	224	-52	211.1	4.6
5	Kaikoura	19.8	13.4	200	-68	131.9	4.4
6	Mcleans	19.7	9.9	187	-69	97.1	1.9
7	North Bank	19.6	9.4	181	-65	226.4	1.2
8	Makikihi	19.3	10.34	167	-72	104.3	2.6
9	Mayfield	18.5	7.8	120	-62	63.6	1.0
10	Birch Hill	16.9	8.3	162	-42	292.1	0.1
11	Ashley For.	16.1	9.0	154	-70	98.4	0.9
12	Blenheim	15.0	10.9	197	-60	200.5	2.4
13	Woodend	14.6	9.7	177	-66	77.5	2.3
14	Moeraki	14.0	9.9	138	-71	44.5	1.0
15	Waimate-10	12.6	8.5	158	-75	93.1	1.0
16	Salt Water Cr.	12.4	10.9	177	-66	88.1	2.3
17	Rakaia	11.5	9.9	148	-74	90.6	2.9
18	Awatere Valley	11.5	10.4	195	-50	142.9	0.1
19	Spotswood	10.3	9.8	179	-40	149.1	0.6
20	Oamaru	10.1	9.7	142	-70	46.9	3.2
21	Wairau Valley	10.0	9.1	194	-33	303.6	0.7
22	Rangitata	10.0	8.6	177	-71	114.8	2.6
23	Waimate-12	9.5	8.5	158	-75	93.1	1.0
24	Argyle	9.3	7.8	159	-60	279.6	-0.8
25	Winchmore	9.0	8.4	163	-69	89.2	1.1
26	Lincoln	8.3	9.3	169	-70	68.8	2.9

27	Rangiora Nursery	7.9	8.9	171	-59	97.0	1.5
28	Kurow	6.5	8.7	125	-71	60.6	-0.6
29	Spencerville	6.4	9.8	190	-71	89.8	3.1
30	Lake Waihola	5.9	10.2	108	-16	69.2	1.5
31	Merivale Station	5.4	5.9	165	-62	71.3	-0.9
32	Orari	5.2	8.5	163	-81	93.0	1.0
33	Amberley B.	5.1	10.9	158	-78	196.6	2.3
34	Homebush	5.0	6.6	148	-60	59.5	-0.02
35	Amberley	4.8	10.0	158	-52	196.6	2.3
36	Tapanui	4.7	6.25	68	-44	146.8	1.0
37	Darfield	4.6	8.4	212	-44	165.3	0.5
38	Cromwell	4.5	7.8	178	-57	113.4	-1.5
39	Balmoral	4.1	9.2	160	-43	83.6	-0.3
40	Eyrewell-Wrights	3.9	8.5	210	-60	160.4	-0.3
41	Burkes Pass	3.8	6.5	195	-69	287.7	-1.8
42	Wanaka	3.7	6.4	118	-15	98.8	-0.2
43	Hanmer	3.3	6.8	179	-40	149.1	-1.2
44	Eyrewell - Downs	3.1	9.3	175	-59	82.9	0.3
45	Dunsandel	2.9	8.6	184	-62	94.2	2.2
46	Crown Range	1.8	5.2	77	-25	39.1	0.0
47	Dunback	1.6	4.4	35	-18	6.6	-2.1
48	Dunedin	1.2	8.5	46	-19	11.8	-2.0
49	Tara Hills	1.2	5.2	142	-64	96.2	-1.7
50	Glynn Wye	1.1	5.0	112	-24	90.8	-0.8
51	Hororata-West	0.9	5.9	202	-25	158.5	0.2
52	Low Mount	0.0	7.4	123	-20	28.2	-1.3

[1] Mean daily minimum temperature for February 1992.
[2] Total rainfall for the period August through to November 1991.
[3] Total daily water stress (intergral) for both February and March 1992.
[4] Total daily growing degree days (GDD) for the period August through to November 1991, base temperature 10°C.
[5] Mean daily minimum temperature for May 1992.

Table 4.7

Table of soil classification, across the 52 sites sampled in 1992. The information for each soil class was obtained directly from the literature.

Sites sampled in (1992)	Mean No strobili	Soil class	Soil texture	Soil pH	Soil phosphate
Rabbit Island	31.9	8	1	6.3	3.0
Motueka	28.4	5	4	5.1	0.0
Appleby	24.2	5	4	5.1	0.0
Grassmere	20.1	7	3	6.1	1.6
Kaikoura	19.8	8	1	5.4	5.4
Mcleans	19.7	7	3	5.9	21.0
Northbank	19.6	6	4	5.5	1.0
Makikihi	19.3	7	4	5.7	1.0
Mayfield	18.5	5	4	4.8	14.0
Birch Hill	16.9	5	5	5.0	12.0
Ashley For.	16.1	5	4	5.7	1.0
Blenheim	15.0	7	3	5.4	5.4
Woodend	14.7	8	1	5.5	18.0
Moeraki	14.0	5	5	5.9	7.8
Waimate-10	12.6	7	4	6.0	2.0
Salt Water Cr.	12.4	8	1	5.5	18.0
Rakaia	11.5	3	4	5.5	7.0
Awatere Valley	11.5	5	3	6.0	10.0
Spotswood	10.3	2	4	5.5	4.0
Rangitata	10.0	3	4	5.4	4.0
Oamaru	10.1	7	4	6.2	11.0
Wairau Valley	10.0	2	3	5.2	9.0
Waimate-12	9.5	7	4	6.0	2.0
Argyle	9.3	5	3	6.0	4.0
Winchmore	9.0	2	4	5.5	5.0
Lincoln	8.3	2	4	5.5	5.0

Rangiora Nursery	7.9	7	5	5.9	2.0
Kurow	6.5	7	3	6.0	7.0
Spencerville	6.4	8	1	5.5	18.0
Lake Waihola	5.9	8	3	7.8	26.0
Merivale Station	5.4	2	3	5.8	10.0
Orari	5.2	3	3	5.4	28.0
Amberley B.	5.1	8	2	5.5	11.0
Homebush	5.0	2	4	5.5	5.0
Amberley	4.8	2	4	6.4	1.0
Tapanui	4.7	5	4	5.5	6.0
Darfield	4.6	2	4	5.7	4.0
Cromwell	4.5	1	3	9.4	40.0
Balmoral	4.1	2	3	5.6	8.0
Eyrewell-Wrights	3.9	2	4	5.5	5.0
Burkes Pass	3.8	5	4	6.1	1.0
Wanaka	3.7	1	2	6.8	2.0
Hanmer	3.3	5	4	5.0	13.0
Eyrewell - Downs	3.1	7	5	6.0	7.0
Dunsandel	2.9	7	5	5.5	7.0
Crown Range	1.8	7	4	6.2	3.0
Dunback	1.6	3	4	4.9	1.0
Dunedin	1.2	2	4	5.0	4.0
Tara Hills	1.2	4	3	5.9	5.0
Glynn Wye	1.1	4	4	5.4	0.0
Hororata-West	0.9	5	5	5.2	8.0
Low Mount	0.0	3	4	5.5	1.0

Soil variable	Correlation coefficient (r)
Class	0.40 (p<0.0032)
Texture	-0.20 (p<0.1441)
Phosphate score	0.01 (P<0.9494)
pH	-0.051 (p<0.7155)

The soil class scores mean the following:

1 = Brown grey earth.
2 = Yellow grey earth.
3 = High country yellow brown earth.
4 = Upland yellow brown earth.
5 = Intergrade yellow grey earth.
6 = Yellow brown earth.
7 = Recent soil.
8 = Yellow brown sands.
9 = Gley soils.

The soil texture scores mean the following:

1 = Sand
2 = Loamy sand
3 = Stoney intergrade between sand and silt.
4 = Sandy loam.
5 = Stoney sandy loam.
6 = Silt loam.
7 = Clay loam.

The soil phosphorous [1]scores mean the following:

>22	Very high
16-22	High
6-12	Medium
2-6	Low
<2	Very low

[1] **Citric soluble phosphate in 2% citric acid.**

D. DISCUSSION.

Across the 52 sites where data were collected, the number of emergent strobili in the top 2 metres of the crown ranged from 0 to 31.9, with a mean of 9.6 and a mean standard deviation of 8.0. The differences between sites were highly significant, with the most productive site having a strobilus count 3.3 times that of the mean site. That level of variability is comparable with that reported in Sweet (1975).

The number of sites sampled proved adequate for obtaining sufficient data for developing a predictive model. A "rule of thumb" is to make 10 times more observations than variables in the model (Hair *et al.*, 1979).

Around 65% of the variability in numbers of emergent strobili across sites was explainable statistically in terms of climate and soil moisture variables. While that percentage is more than adequate for purposes of a predictive model, it is interesting to reflect on the residual 35%. Clearly with an overall standard error of ±1.26 a significant proportion of variance between sites was unlikely to be due to the sampling method. While it is beyond the capacity of this chapter to speculate effectively on the content of that 35%, it should be noted that it was not possible to obtain information on the genetic origins of the stands. The other feature which has been implicated in strobilus production in the literature, but not measured in this Chapter is that of mineral nutrient levels.

While it was largely beyond the scope of this study to consider soil mineral nutrition effects on strobilus production in detail, it was considered feasible to gain some knowledge on soil fertility across sites by using soil type classifications published in the New Zealand Soil Bureau Bulletins (see Materials and Methods for Bulletin numbers). These classifications were then used to establish a theoretical soil phosphate level as well as a pH: the latter may determine the availability of various macro- and micro-nutrients. Ideally, it would have been desirable to have more general information on other key mineral nutrients for each soil class. Unfortunately this sort of data is not readily obtainable.

The correlation analysis, however, indicated hat there was little agreement between strobilus number and the data for soil phosphate level and pH. Essentially there was no suggestion that soil fertility was associated strongly with the counts of strobili across sites. Nevertheless it

should be borne in mind that the soil class data used in this analysis were only theoretical: they were obtained directly from the literature. It may be that some of the soils were incorrectly classified, remembering that soil maps in some parts of New Zealand do not account for subtle soil boundary changes. A further factor that may have confounded the fertility data is that sites may have had a previous soil ameliorative fertiliser history.

The soil classes were significantly correlated with strobilus counts. This, however, was likely to be more of a reflection of the climate in which the soils developed, rather than soil fertility. The soil classification system in New Zealand has been developed such that soils are organised into groups having common diagnostic properties. One of the major soil forming factors that bring about those diagnostic properties is climate; thus soil classes in the various parts of the country are associated with various temperature and rainfall regimes.

The higher counts of strobili were recorded in the north of the South Island where temperatures are mild and moisture often limiting and the soils are generally classed as yellow brown earths, yellow brown sands and recent soils. Lower counts were recorded in the south of the South Island where in the cooler moister regions the soils are generally classified as brown grey earths, yellow grey earths, or at higher altitudes where the high country yellow brown earths are found. The classes are not necessarily indicative of soil fertility.

From this study there was some indication that soil mineral nutrients are not strongly linked to strobilus production as high strobilus counts were recorded frequently at sites comprising sands which are generally infertile. Because of the structure of sands they have a poor ability to retain mobile nutrients. On the other hand low counts of strobili were recorded at the more fertile southern sites, for example, in Canterbury and South Canterbury. It is likely that temperature and moisture effects on strobilus production are so predominant that they mask out any obvious effects of soil fertility, providing it is at a level that healthy tree growth can be sustained. For example, the sands are probably moisture depleted more often than the heavier fertile silt/loam soils.

In terms of the published soil phosphate levels the sites in the North, particularly around Nelson, had the lowest levels of any of the sites in the survey and yet they were in the top 10 strobilus producing sites. If the data are authentic, then it does not indicate that soil P plays a major role in strobilus production.

Subject to satisfactory validation (see Chapter 5), the model explains sufficient of the variability in emergent strobilus number to constitute an effective predictive tool for seed orchard location. However, some of the parameters (such as soil water stress integral) are not easily developable across New Zealand as a whole. In that respect, it is fortunate that 54% of the variability in emergent strobilus number is explainable by mean minimum February temperature: a variable which is recorded at all meteorological stations.

The contribution to the model of mean minimum February temperature is one that is generally predictable in terms of the broader literature (Eriksson, 1982). While it is generally accepted that increasing temperature at the time of strobilus initiation increases strobilus production, it should be remembered that much of the literature was based on boreal forest species, and radiata pine evolved in a totally different temperature regime to these. It also needs to be remembered that the sites sampled in this Chapter were all South Island ones, and that the relationship with temperature may not hold in some of the warmer parts of the North Island. That possibility needs to be checked out in the validation of the model (see Chapter 5).

The second term in the multiple regression, the total degree days in the 5 months prior to long shoot initiation, weighted against rainfall, is again logical in terms of existing knowledge. Long shoots are initiated on vigorous shoots in the upper parts of the crown (Owens and Blake, 1985). A number of the treatments in the literature which have successfully increased strobilus production are believed to have done so by increasing the number of buds in the crown which are competent to initiate long shoots. Favourable temperature and moisture in the months preceding long shoot initiation can be expected to do that.

The literature generally equates strobilus initiation with an increased level of stress (e.g., by root pruning); and water stress is often regarded as an agent which contributes to flowering in woody plants (Matthews, 1963). In this model, the soil water stress integral at the time of long shoot development, while correlated with emergent strobilus numbers was negatively correlated. That is, sites with a higher water stress during the time of strobilus differentiation carried more strobili than those with less water stress.

The final component of the model is the mean minimum temperature for May which, although with a high correlation coefficient, was significant only at the 10% level in the model as a whole.

Recalling the correlation of mean minimum May temperature with counts of strobili was 0.68 and that for mean minimum February was 0.74, it may seem strange that May temperature was not a significant independent variable in the model. One of the major reasons for this is that both these temperature variables were correlated with each other. Nonetheless they were considered to be each causing individual effects on the differentiating seed-cone buds. For this reason it was decided to run them both in the regression analysis, but realising that they were autocorrelated and were likely to be explaining the same proportion of the variance.

In multiple regression analysis individual independent variables can be selected into the model on the basis of a range of statistical tests (F-statistic, partial correlation coefficients, maximum r) or by the experimenter on the basis of biological understanding of how the independent variable may be related to the dependent variable. For this Chapter a stepwise forward selection procedure was used and the independent variables were selected on the basis of the F-statistic; i.e., each independent variable was selected on the F-statistic that reflected the variable's contribution to the model if it was included - i.e., the amount of reduction in the mean square error term through the inclusion of the variable.

Variables that are highly correlated with a dependent variable are not necessarily selected as a significant independent variable in a multiple regression model. Although a variable may have a high simple correlation coefficient when correlated with the dependent variable relative to the other independent variables, it may have a low partial correlation value, particularly if it is autocorrelated with an independent variable already selected into the model.

Mean minimum February temperature had the highest simple correlation of all the independent variables and thus was selected into the model first; at step one the partial correlation variable for February was same as the r value. Because mean minimum May temperature had a smaller (although high) correlation coefficient, it was not selected at step 1 ahead of February. This meant that mean minimum May temperature, because it was to some extent autocorrelated with mean minimum February temperature was unable to account for a significant amount of the unexplained variance, relative to the other independent variables. That is, mean minimum May temperature had a non-significant partial correlation coefficient relative to the other independent variables that were accounting for a different, but significant, part of the unexplained variance.

As indicated above, the climatic variables tested in the model are those which were expected, on the basis of the literature, or on the findings reported in Chapter 3, to be correlated with strobilus emergence. It may well be that other climatic or site variables which were not tested are also correlated with strobilus number. Attempts will be made experimentally to explore some of these issues in subsequent chapters.

A question which was asked early in the study relates to the polycyclic nature of radiata pine. The initiation of multiple cycles in the annual shoot growth offers the opportunity to initiate multiple cycles of strobili. Are the sites with high numbers of emergent strobili simply those sites which are highly polycyclic? Or are they sites where a large number of long shoots are initiated in the first cycle, many of which in turn develop into strobili? Or perhaps a combination of both factors? These issues are addressed in Chapter 6.

As a whole, the model developed in this chapter has indicated some climate and site attributes which are statistically related to emergent strobilus production. Those attributes are able to be explored experimentally, to further our knowledge of the biological basis of strobilus production; and this will be done in subsequent Chapters. The model also, once validated, offers the opportunity to predict the parts of New Zealand where strobilus production in seed orchards may be optimal. This too will be done in subsequent Chapter 5.

CHAPTER 5

MODEL VALIDATION AND SITE PREDICTION

A. INTRODUCTION

Good science practice dictates that when a predictive model is developed, it should be validated across a range of sites which were not used in the development of the original model.

When the model reported in Chapter 4 was developed, the sites selected were restricted to the South Island, east of the main mountain ranges. While one reason for restriction to the South Island was financial and logistical, all available evidence indicated that the South Island included both the most and least productive sites in New Zealand for strobilus production. Within the South Island, the restriction to the eastern side was because of an expectation that soil moisture would have a significant effect on strobilus numbers. Essentially, the east side of the South Island is a rain shadow area, while the west side has high rainfall. It was thought that to incorporate data from both sides of the Southern Alps would reduce the capacity to determine relationships other than those based on soil moisture.

Having developed the model in Chapter 4, it became clear that soil moisture was not a key component of the climatic factors affecting strobilus numbers. The fact that temperature was the key variable, and that the North Island in general is warmer than the South Island raised questions as to whether the temperature relationships derived would 'hold' in warmer areas.

Thus in validating the model, the decision was taken to both: (i) select new sites within the original South Island area east of the main ranges; and (ii) select sites in the North Island which would extend the model in temperature terms, and ascertain its limits.

B. MATERIALS AND METHODS

1. The Sites

In 1994, 22 sites growing stands of *Pinus radiata* between the ages of 10 and 12 years old were selected, 12 along the east side of the main dividing range of the South Island and 10 in the North Island of New Zealand. Stands were selected on the basis of the same criteria as in Chapter 4, although in the validation, care was taken only to select stands within 2 km of a climate recording station, thus eliminating the need to correct temperature for altitudinal differences.

The sites chosen are listed in Table 5.1 and mapped in Figure 5.1. They range in latitude from 35°46'S to 48°16'S, and in altitude from 2m to 610m above sea level. The North Island sites are from both east and west coasts.

Table 5.1

Location and height above sea level of the 22 model validation sites. The sites are listed in descending order according to strobilus counts.

No	Site	Latitude	Longitude	Altitude
53	Ngunguru	35°46'S	174°22'E	37.0
54	Wairoa	39°00'S	177°24'E	8.0
55	Woodhill	36°45'S	174°26'E	30.0
56	Nelson	41°17'S	173°14'E	2.0
57	Grassmere-2	41°44'S	174°09'E	4.0
58	Cape Campbell	41°44'S	174°17'E	3.0
59	Dannevirke	40°13'S	176°07'E	207.0
60	Oamaru-2	45°07'S	171°00'E	20.0
61	Hanmer-2	42°31'S	172°51'E	386.0
62	Mohaka	39°04'S	177°02'E	286.0
63	Matakana	37°35'S	176°12'E	4.0
64	Kirwee	43°50'S	172°10'E	192.0
65	Havelock Nth	39°40'S	176°53'E	9.0
66	Balclutha	48°16'S	169°44'E	8.0
67	Cromwell-2	45°02'S	169°12'E	213.0
68	Levin	40°39'S	175°16'E	46.0
69	Murupara	38°27'S	176°42'E	198.0
70	Peel Forest	43°54'S	171°16'E	274.0
71	Mosgiel	45°56'S	170°12'E	3.0
72	Lumsden	45°45'S	168°20'E	200.0
73	Martinborough	40°55'S	175°50'E	57.0
74	Naseby	45°01'S	170°06'E	610.0

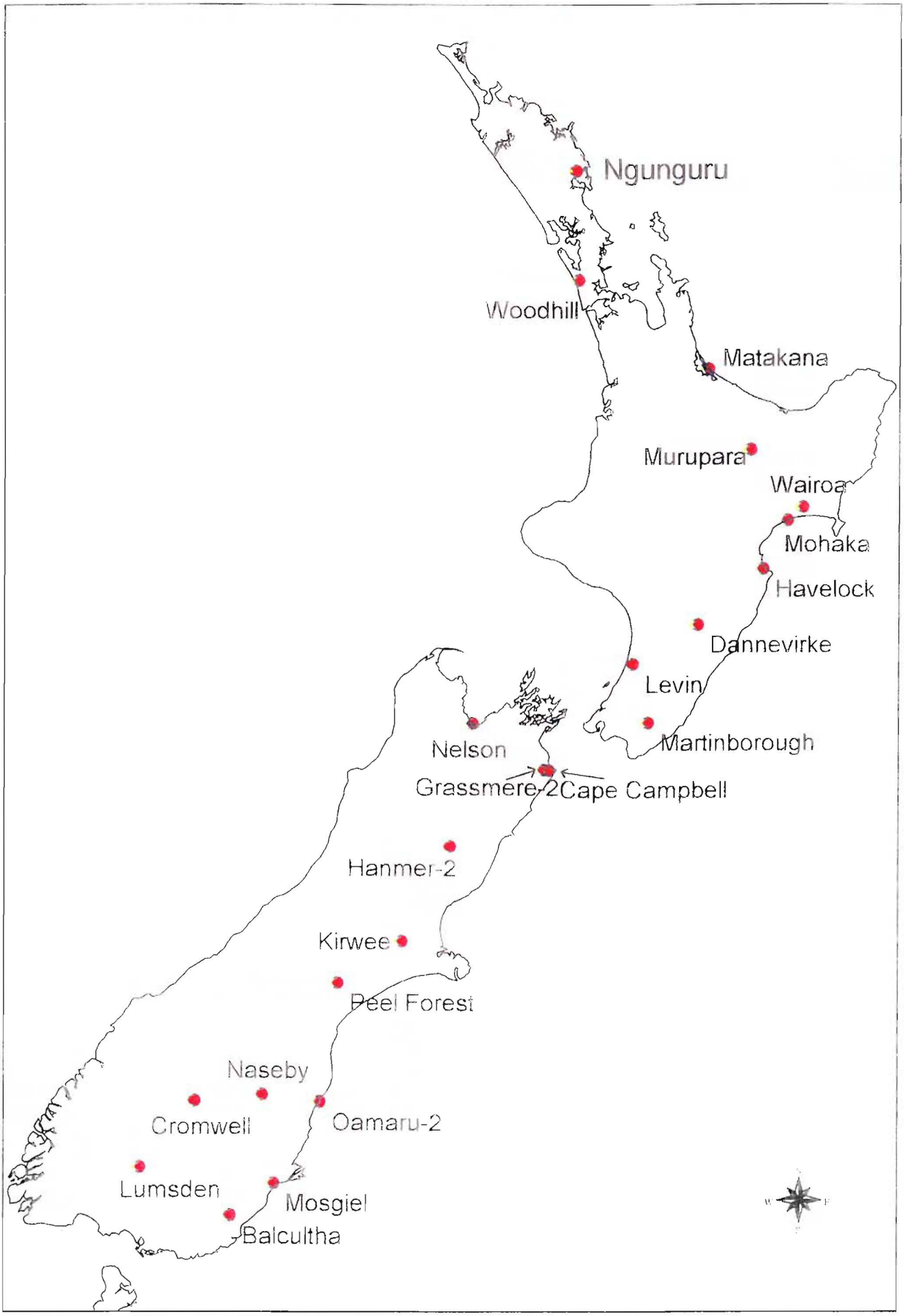

Figure 5.1

A map of New Zealand illustrating the location of sites at which strobilus counts were made in 1994.

2. Strobilus Counts and Long Shoot Primordia Assessment

During October 1994, counts of strobili were made at each site, using the sampling methodology described in Chapter 3. In February 1994, 6 terminal buds were also sampled from each site. They were clipped, 1 per tree, from potential strobilus-bearing branches, using high pruning secateurs. Buds were stored for 24hrs in FAA and then in 70% ethanol until dissection when the number of long shoot primordia within each bud was counted, using a binocular microscope.

3. Climatological Data

3.1 1994 Data

The appropriate (1993/94) climatological data (as used in Chapter 4) were obtained from N.I.W.A. for each site. The root zone soil water stress integral (for February and March 1994) was calculated for each site using the soil water balance model (and methodology) described in Chapter 4. The accumulated GDD (thermal time) for August 1993 through to November 1993 was also calculated as for Chapter 4, and this value was corrected for rainfall.

3.2 Long Term Data for Both 1992 and 1994 Sites

In a later part of this chapter, the need was seen to utilise long-term mean minimum temperature data for February for each site.

In 1987 the NZ Meteorological Service was substantially re-structured and downgraded in budgeting terms. The type and quality of meteorological data collected was reduced with a number of stations being terminated, and a few new ones initiated. The most recent comprehensive set of long-term (<30 years) data exists in the New Zealand Meteorological Service's 1983 publication "Summaries of Climatological Observations to 1980". That publication was used for all long-term data.

All climatic data were written into a Quattro Pro (version 5.0 for DOS) spreadsheet where it could be used with the predictive model developed in Chapter 4, as with other climatic data.

4. Statistical Analysis

Validation of the model was done using PROG REG and PROC GPLOT procedures (SAS Institute, 1987).

For validation, the residual values (difference between actual and predicted values) were calculated for each site. They were then plotted against the actual (observed) values. To check for model bias a regression line was fitted to the residuals along with 95% confidence limits.

Initially the complete model was validated for the 12 South Island sites and then for all 22 validation sites.

Following validations both the 1992 and 1994 databases were combined. The strobilus data were then re-modelled using a stepwise multiple regression procedure (see Chapter 4). This analysis again identified mean minimum February temperature as a key variable regarding strobilus production and that there was some indication that the relationship between these two variables may be non-linear. To explore this further, the following non-linear growth functions were fitted to the data:

(i) Schumacher: $y=\exp(\alpha-\beta/T)$ (see Schumacher, 1939; Whyte and Woollons, 1990).

(ii) Hossfields: $y=\alpha T^{\gamma}/\alpha\beta+T^{\gamma}$ (R.C. Woollons, pers. comm.).

(iii) Modified Gompertz: $y=\exp(\alpha-\beta\gamma^{T})$ (see Causton, 1977; Whyte and Woollons, 1990).

A logistic function in the form of y=a/1+exp(c+bx) was also fitted to the data. For each equation the parameters were approximated by iterating the best fit using the PROC Nlin procedure (SAS Institute, 1987).

5. Site Predictions in New Zealand

Two different systems exist to develop a mean minimum temperature map of New Zealand. Firstly, a temperature map can be generated using a geographic information system (GIS) (see Barringer, 1995).

A multiple regression model for mean minimum February temperature was linked with a regular grid digital terrain model (DTM) and a PC-based GIS system to derive the map.

A semi-empirical multiple regression model for calculating mean minimum February temperature with respect to altitude, latitude and distance from the coast was derived from temperature normals calculated for the 1951 to 1980 period (New Zealand Meteorological Service, 1983) (Norton, 1985). The normals represented the mean value for minimum temperature for February over a 30 year period. Normals were calculated for 346 temperature recording stations in New Zealand.

The DTM resolved down to 500m × 500m regular grids and the data was in a format suitable for importing as a raster layer in the GIS.

Once the grid based DTM had been imported to the GIS it was used to estimate latitude, longitude and distance from the coast for every raster cell. The mean minimum February temperature within each cell was then estimated by the multiple regression model (Norton, 1985).

Secondly, a climate model developed for New Zealand has been developed by Dr Neil Mitchell of the University of Auckland based on climate data recorded at the various meteorological stations of the New Zealand Meteorological Service. The model consists of a number of interpolated climate surfaces relating respectively to solar radiation, precipitation, maximum temperature, and minimum temperature, which were produced using algorithms developed by Hutchinson (Mitchell, 1991). The BIOCLIM programme (Nix, 1986) is used to interrogate the surfaces to obtain estimates of climate parameters at each required location. Full details of the modelling procedure have been published by Mitchell (1991).

Both the GIS mapping system and the Mitchell model were used, by courtesy of their developers, to develop a mean minimum February temperature map for New Zealand. Because the temperature map generated by each of the methods had subtle differences, particularly in the warmer northern region, it was considered appropriate to include both maps in this thesis.

C. RESULTS

1. Climatic Data and Strobilus Counts Across Sites

These data are presented in Tables 5.2 and 5.3.

The numbers of strobili counted differed significantly between sites. Across the 22 sites sampled in 1994 the mean number of strobili in the top 2 metres of crown was 22.8±2.23 ranged from 0.8 to 55.4. The average number of strobili counted at the six highest-producing sites was 40.7. Table 5.3 presents the climatic data for each site which are relevant to the strobilus prediction model developed in Chapter 4.

2 Model Validation in the South Island

Figure 5.2 presents a graph of the validation process as described in section 4 of the Materials and Methods.

The model reported in Chapter 4 predicted the counts of strobili across the eastern South Island accurately. The residual values (difference between actual counts and predicted counts) were randomly distributed around the reference line (the fitted line if the predicted and actual counts were exactly the same). This result indicates that the model had little bias; that is there was no relationship between the actual counts and the residuals; the r^2 value for this relationship was 0.0003. There was no suggestion that for low strobilus-producing sites the model was either under or over predicting, and similarly for high strobilus-producing sites.

The mean actual counts of strobili across the South Island sites was 19.25 and the mean predicted value for those sites was 16.66. Most of the residual values fell within the 95% confidence bounds, although 3 sites (Cape Campbell, Oamaru-2 and Hanmer-2) did not, indicating that there was significant modelling error relating to these sites. (N.B. the confidence boundaries are indicated by curved lines as at the extremes the estimates are less precise - moving away from the mean X,Y value along the regression line) (Figure 5.2).

3. Model Validation Using All 22 Sites

When the North Island sites were included the model no longer predicted strobilus numbers so accurately.

The residual values were less randomly distributed around the reference line (Figure 5.3). A relationship was found between the residual values and the actual counts indicating that the model had some bias. It was tending to over estimate on the high strobilus-producing sites. The fitted regression line to the residual data had a r^2 of 0.66 with a slope of -0.37 indicating again that for the better strobilus-producing sites predictions were greater than actual counts. However, the slope of the fitted line was not statistically (t-statistic) different from that of the reference line.

4. Correlations of Climatic Variables with Counts of Strobili for the North and South Island Sites

Despite the model over-predicting for the warmer North Island sites, the fact that a validation regression line did not differ significantly in slope allowed the validation plots to be combined with the original (Chapter 4) data source. This was done and new correlations developed for the combined data. These correlations are presented in Table 5.4.

Correlation analysis indicated again that mean minimum temperature for February of the year counts were made was the most highly correlated variable with strobilus counts, with the mean of 30 year data for this variable having only a slightly lower r-value. The May temperature variable was also highly correlated, although slightly less so than that of February. The variables G_r and S_ψ were less correlated with strobilus number, with the correlation coefficient for the soil water stress integral being not significant.

5. Re-Modelled Strobilus Data

The new model for the combined data was similar to the 1992 one in the amount of variance accounted for, although it selected fewer variables (see Table 5.5).

The stepwise regression analysis selected the February temperature variable into the model first and then respectively the G_r variable and the May temperature variable. The first variable accounted for around 56.6% of the between site variance and a further 2.7% was accounted for by G_r and 2.3% by May temperature giving a total of approximately 62%. This was equivalent to that accounted for by the 1992 model (see Chapter 4).

Figure 5.4 showed that overall the residual values (predicted - actual) were randomly arranged. There was little indication that the model had any bias. The slope of the fitted regression line was not significant (r^2=0.001). The mean value of the residuals was 0 and the standard deviation was 0.54. Most of the residuals were within 2 deviations.

6. February Model

The preceding linear models were useful tools for identifying variables that were associated with strobilus production. In all the preceding models mean minimum temperature for February accounted for around 50% of the between site variance in strobilus production. It was found that a simple linear regression between strobilus number across 74 sites, and long term February temperature accounted for 56.6% of the between site variability (Table 5.5).

The fact that a simple linear regression such as that can explain over half of the variability offers a useful capability to screen potential new seed orchard sites. A desirable requirement for such a prediction is that it be possible with existing information. The use of parameters such as soil water stress integral and accumulated growing degree days do not fit this requirement, and thus there are strong reasons to use long-term mean minimum February temperature as a sole predictor of strobilus production. It was fortunate that data (long term) is readily obtainable for this variable across a large number of climate recording sites, and based on the correlation analysis this relationship holds for either short term or long term February temperature data (Table 5.4).

The next approach was thus to explore whether the relationship between strobilus number and long-term mean minimum February temperature was better described by a non-linear function. Until now the linear models best modelled strobilus production patterns when strobilus data were $\log_e$-transformed. This indicated that a non-linear (e.g., sigmoid) function may more appropriately describe the relationship between the February temperature variable and strobilus

counts.

Although the exponential (logistic) equation fitted the data the parameters a, b and c were not significantly different from 0. However, it was found that the Schumacher sigmoid growth function satisfactorily fitted the data (see Figure 5.5); the equation parameters α and β were significantly different from 0. These two parameters for the function were estimated using the PROC NLIN procedure in SAS.

The Schumacher function used was as follows:

Strobilus number = exp(α -β/ Feb temp) where:

α=6.76; and
β=45.16 (see Figure 5.5).

The major rationale for fitting a non-linear function lay in the observation that the model was over-predicting and under-predicting strobilus numbers on, respectively, high and low temperature sites. There were only limited sites represented in the data base with a mean minimum February temperature greater than 15°C or lower than 7°C: insufficient to provide a clear indication of strobilus initiation behaviour on these more extreme sites. But common biological understanding suggests that the relationship between strobilus production and temperature cannot remain linear indefinitely. Fitting a Schumacher sigmoid growth function recognised that understanding.

The mean residual value for the Schumacher equation was 0.30 and the standard deviation was 7.07 (Figure 5.6). Most of the residual points were within 2 standard deviations. There was some indication from the residuals that the non-linear model was tending to under estimate counts at the warm sites in the north - probably a reflection of too few data points in this temperature range to accurately fit the curve.

Although a coefficient of determination (r^2) was calculated for the Schumacher equation it was advised that, due to bias it was not appropriate to use this coefficient value to measure the level of fit of the non-linear model. Observing residual plots is seen as a superior method for determining the appropriateness of a non-linear model (R. C. Woollons, pers. comm.).

7. Presence of Long Shoot Primordia

The mean numbers of long shoot primordia per bud from each site are presented in Table 5.6. The data indicate that at harvest time (between February 6 and 22, 1994) potential strobilus bearing shoots had initiated long shoot primordia, at all sites except Martinborough, Lumsden and Naseby. Those sites were the lowest strobilus producing sites of the 22 sampled in the validation.

8. Prediction of Sites Countrywide

There are marked differences in mean minimum February temperatures between the North and South Islands. Both Figures 5.7 and 5.8 (and Appendix E) are in agreement that there are no areas of the South Island with mean minimum February temperatures higher than 14°C; and the areas over 12°C are very limited. In the North Island on the other hand, there are substantial areas with temperatures above 14°C, both in the north of the island, and in the coastal fringes further south. Large areas have mean minimum February temperatures in excess of 15°C and a few areas exceed 16°C.

While the two figures are in relatively good agreement regarding the location of areas with mean temperatures below 14°C, their agreement is poorer at that level. However, they are in broad agreement that the areas with the highest mean minimum February temperatures are in the north of the North Island, and along a relatively narrow coastal fringe going further south. The GIS mapping system in particular (Figure 5.7) stresses the significance of the coastal influence.

In the South Island, the places with the highest mean minimum February temperature are in the north, followed by a coastal band up each side of the northern half of the island.

Taken together, the 2 figures offer a clear perspective as to which parts of New Zealand have high mean minimum February temperatures, and thus the potential for high strobilus production.

Table 5.2

Total numbers of emergent strobili across sites in the South Island and North Island. Counts were made in October 1994 on trees aged between 10 and 12 years. At each site the number of strobili in the top 2 metres of crown of 40 trees was counted. Data are presented as mean values.

No	Site - sampled in 1994	Number of strobili	Standard error
53	Ngunguru	55.4	5.56
54	Wairoa	46.0	2.15
55	Woodhill	43.6	2.41
56	Nelson	34.5	3.94
57	Grassmere-2	34.2	3.08
58	Cape Campbell	31.0	2.97
59	Dannevirke	28.0	2.90
60	Oamaru-2	27.8	1.90
61	Hanmer-2	27.6	2.05
62	Mohaka	24.0	1.88
63	Matakana	22.2	2.87
64	Kirwee	21.8	2.63
65	Havelock Nth	20.2	2.72
66	Balclutha	16.3	1.61
67	Cromwell-2	16.2	1.88
68	Levin	15.0	2.32
69	Murupara	14.0	2.03
70	Peel Forest	7.7	1.05
71	Mosgiel	6.8	1.34
72	Lumsden	6.3	0.92
73	Martinborough	3.0	0.66
74	Naseby	0.8	0.36
Pr>F (site)		0.0001	
Mean of 22 sites		22.8	Mean SE± 2.23
Range of 22 sites		0.8 - 55.4	

Table 5.3

Mean numbers of strobili and data for the climatic and soil water variables for each site sampled in 1994 in the North Island and South Island.

No	Sites - 1994	Mean No strobili (1994)	[1] Feb temp (°C)	[2] Soil water stress (MPa)	[3] G_r (°Cday)	[4] May temp (°C)
53	Ngunguru	55.4	15.5	-56.5	463.7	10.0
54	Wairoa	46.0	12.3	-51.3	357.3	8.1
55	Woodhill	43.6	15.0	-42.0	422.0	10.0
56	Nelson	34.5	13.1	-63.6	163.7	7.7
57	Grassmere-2	34.2	14.5	-37.9	125.2	7.7
58	Cape Campbell	31.0	14.9	-38.8	74.4	10.6
59	Dannevirke	28.0	11.2	-39.5	156.3	7.7
60	Oamaru-2	27.8	11.7	-10.4	90.7	4.7
61	Hanmer-2	27.6	8.9	-22.5	126.6	2.3
62	Mohaka	24.0	12.2	-57.0	164.7	6.8
63	Matakana	22.2	15.6	-56.2	217.6	9.9
64	Kirwee	21.8	11.5	-32.2	170.0	4.2
65	Havelock Nth	20.2	12.9	-61.7	107.7	6.8
66	Balclutha	16.3	9.8	-37.5	58.8	2.5
67	Cromwell-2	16.2	10.4	-35.6	63.4	1.2
68	Levin	15.0	13.2	-52.7	140.7	8.2
69	Murupara	14.0	13.0	-49.0	47.0	5.0
70	Peel Forest	7.7	9.1	-8.7	120.1	1.3
71	Mosgiel	6.8	9.8	-26.4	75.5	1.8
72	Lumsden	6.3	9.8	-17.4	144.7	3.6
73	Martinborough	3.0	11.9	-42.8	65.6	6.5
74	Naseby	0.8	7.4	-34.7	34.9	0.4

The variables have the following meaning:

[1] Mean daily minimum temperature for February 1994.
[2] Total daily water stress (integral) for both February and March 1994.
[3] Total daily growing degree days (GDD) for the period August through to November 1993, base temperature 10°C weighted against rainfall.
[4] Mean daily minimum temperature for May 1994.

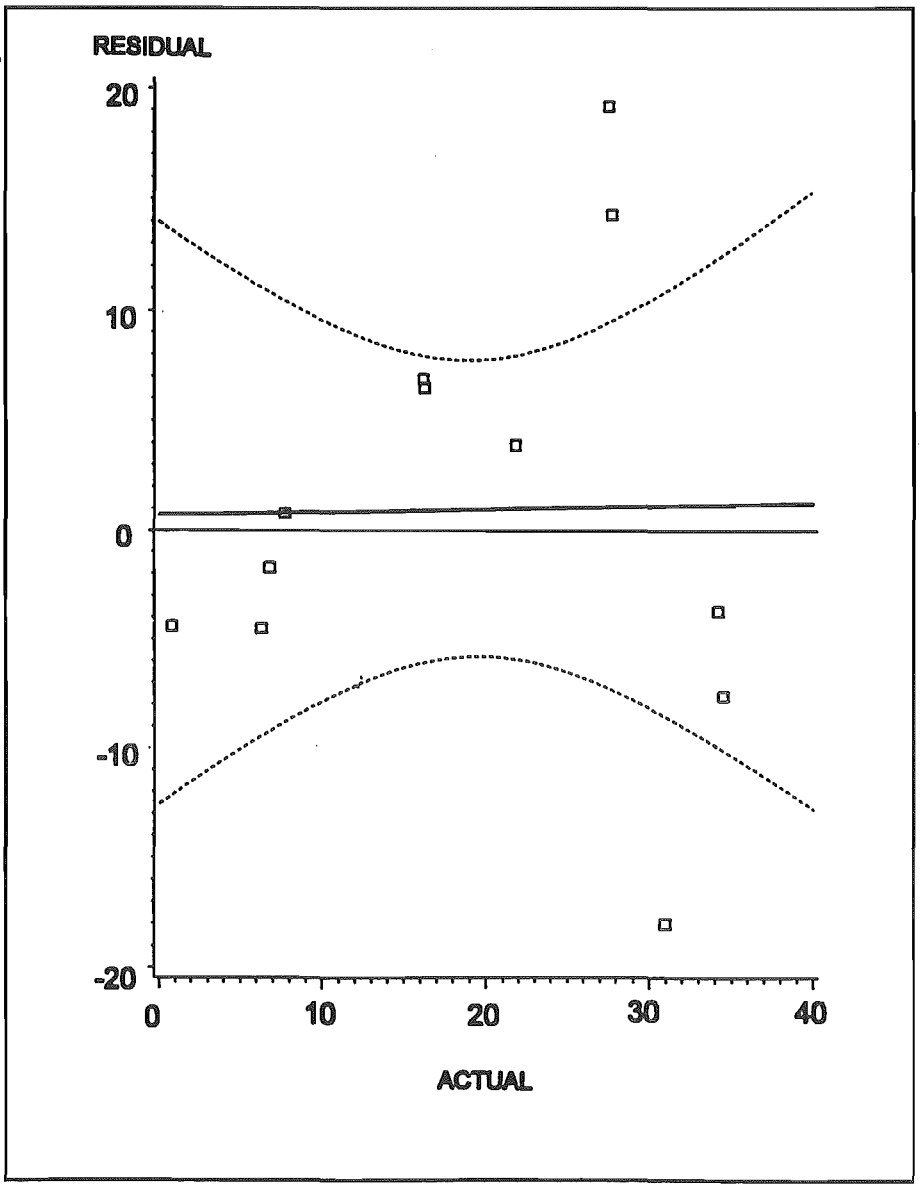

Figure 5.2

A graph of the actual versus residual (actual - predicted) values for the 1992 model predictions across the South Island sites in the 1994 validation study. The dotted, curved lines represent 95% confidence limits.

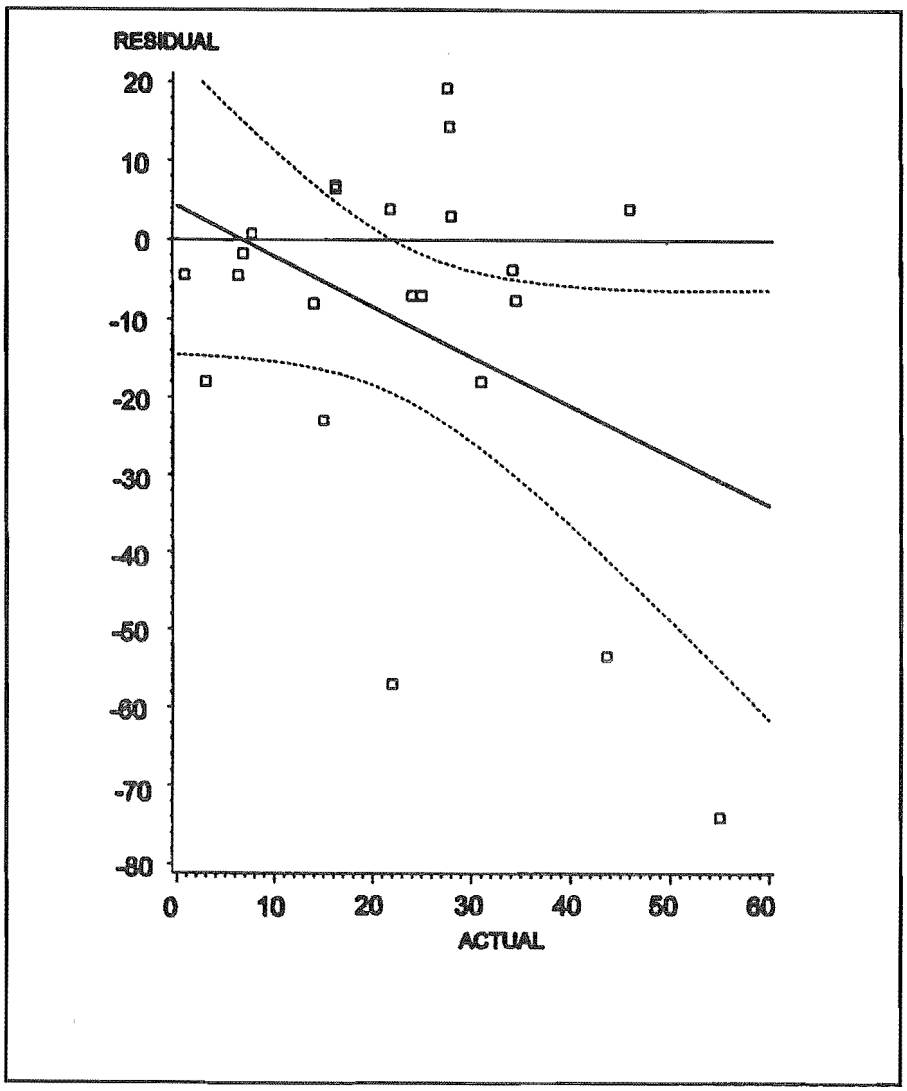

Figure 5.3

A graph of the actual versus residual (actual -predicted) values for the 1992 model predictions across both the North and South Island sites in the 1994 validation study. The dotted, curved lines represent 95% confidence limits.

Table 5.4

Correlations (r) of numbers of emergent strobili (log_e-transformed) with data for climate and soil based variables measured at South Island and North island sites in 1993 and 1994. All correlations were performed using mean data.

Variable	Total numbers of emergent strobili (r)
Feb temp.	**0.765 (p<0.0001)**
Feb temp - 30 years	**0.752 (p<0.0001)**
G_r	**0.521 (p<0.0001)**
S_ψ	**-0.176 (p<0.1331)**
May temp.	**0.702 (p<0.0001)**

The variables have the following meaning:

Feb temp.: mean daily minimum temperature for the February preceding anthesis.

Feb - 30yrs: mean daily minimum temperature for February. The data are long-term means recorded over 30 years.

G_r: accumulated growing degree days (base 10°C) from August to November of the year preceding anthesis, weighted against rainfall for those months.

S_ψ: soil water stress integral (-MPa) for February and March preceding anthesis.

May temp.: mean daily minimum temperature for the May preceding anthesis.

Table 5.5

Table of partial coefficients of determination from stepwise multiple linear regression of log_e-transformed emergent strobili across North and South Island sites. Variables are shown in the order of selection by the regression analysis and the overall model coefficient of determination is given following the inclusion of each variable. Significance levels are also given (p values for the F statistics).

Variable	Sums of squares due to regression	Residual mean square	Pr>F	Coefficient of determination (r^2)
Feb temp.	32.00	0.33	0.0001	0.56
G_r	33.53	0.32	0.0001	0.59
May temp.	34.84	0.31	0.0001	0.62
Total due to regression:	34.84			
Residual sum of squares:	21.62 on 73 df			
Total sum of squares:	56.46			

The four variables listed accounted for around 62% of the overall variation of Y about its mean value. The regression coefficients, together with their standard errors, are listed:

Variable	Coefficient	S.E.
Feb. temp.	0.200	0.063
G_r	0.001	0.036
May temp.	0.074	0.001
Intercept term	-0.176	

The corresponding equation may be written as follows:

Log_e (strobilus) = 0.200 (Feb temp) + 0.001(G_r) + 0.074(May temp) - 0.176

The variables have the following meaning:

Log_e (strobilus) - number of emergent strobili counted in 1992 (South Island) and 1994 (countrywide) log_e-transformed to satisfy regression assumptions.

Feb temp. - mean daily minimum temperature for the February preceding anthesis.

G_r - accumulated growing degree days (base 10°C) from August to November of the year preceding anthesis,weighted against rainfall for those months.

May temp.- mean daily minimum temperature for the May preceding anthesis.

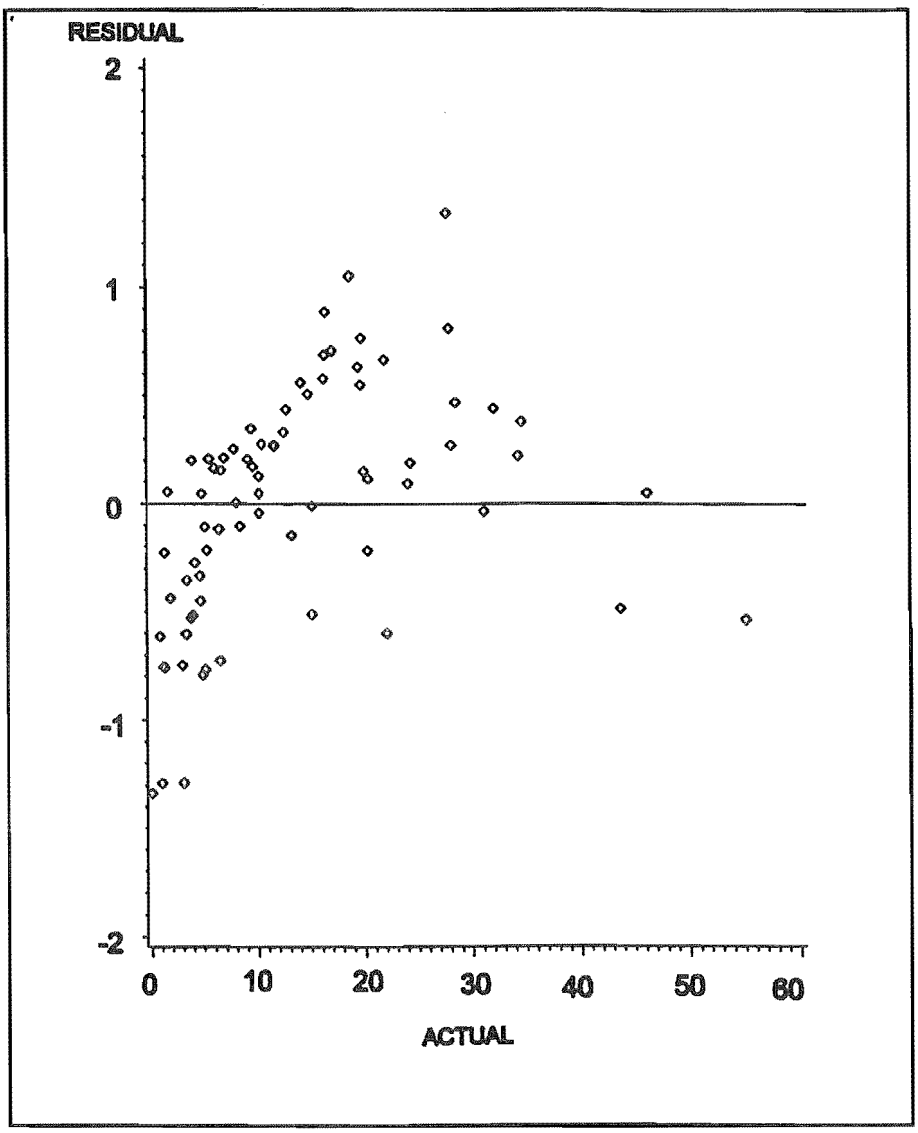

Figure 5.4

A graph of the actual versus residual (actual -predicted) values for the model of the combined strobilus data, collected in 1992 and 1994.

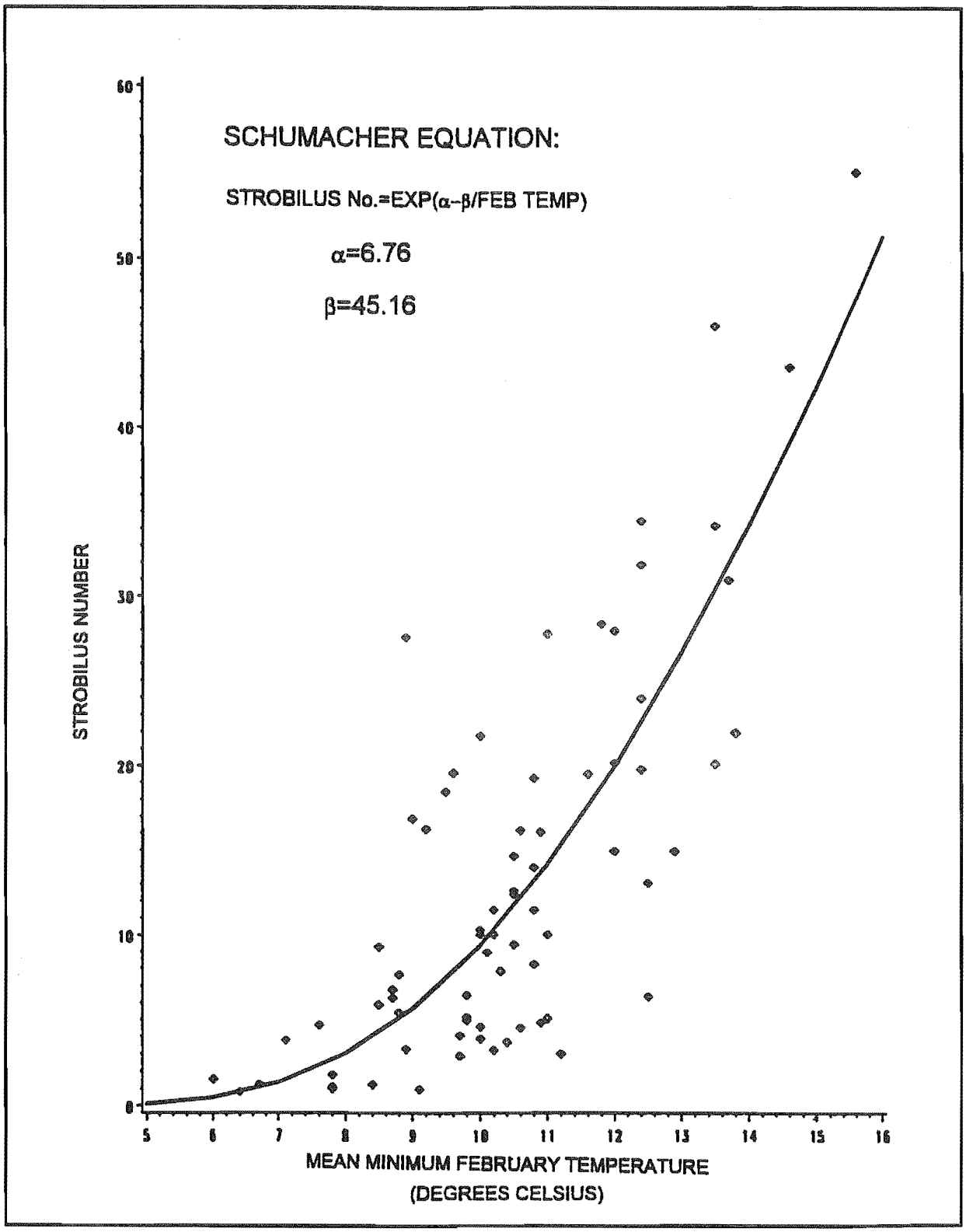

Figure 5.5

The effect of the mean minimum temperature of February on the number of emergent strobili. The temperature data were based on 30 year means lapsed for altitude. The fitted curve is according to a Schumacher equation. The data on strobilus production were collected in 1992 and 1994.

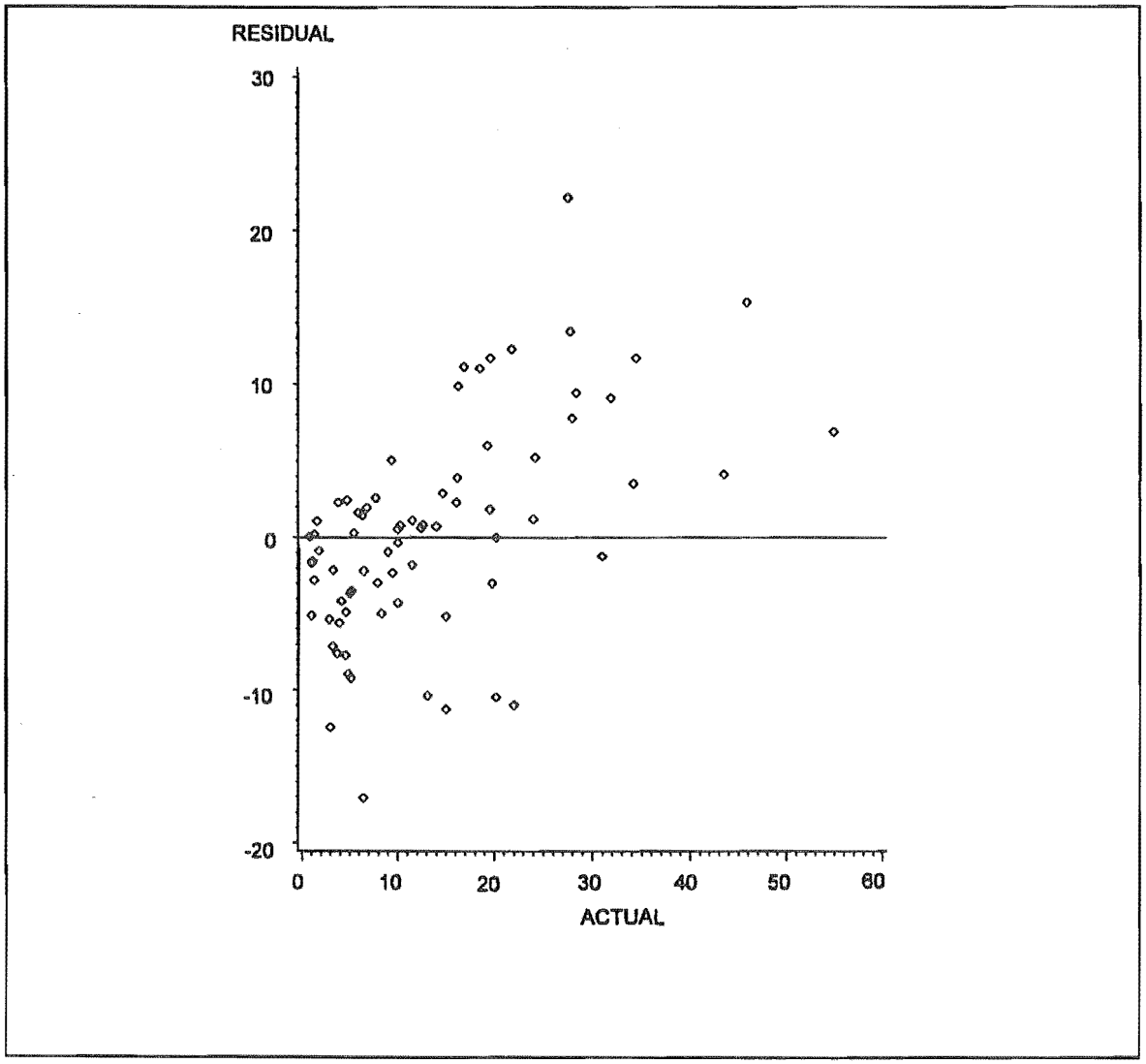

Figure 5.6

A graph of the residual values for the estimates of the Schumacher equation fitted to the 1992 and 1994 strobilus data.

Table 5.6

The mean number of long shoot primordia initiated in the first annual cycle of growth in terminal buds across the 22 model validation sites

No	Site - 1994	Mean number long shoot buds (Feb. 1994)
53	Ngunguru	11.7
54	Wairoa	7.5
55	Woodhill	11.0
56	Nelson	7.3
57	Grassmere-2	9.0
58	Cape Campbell	7.0
59	Dannevirke	6.0
60	Oamaru-2	8.2
61	Hanmer-2	6.4
62	Mohaka	9.4
63	Matakana	6.8
64	Kirwee	8.2
65	Havelock Nth	7.4
66	Balclutha	5.6
67	Cromwell-2	5.6
68	Levin	7.0
69	Murupara	6.4
70	Peel Forest	7.1
71	Mosgiel	5.3
72	Lumsden	n/a
73	Martinborough	n/a
74	Naseby	n/a

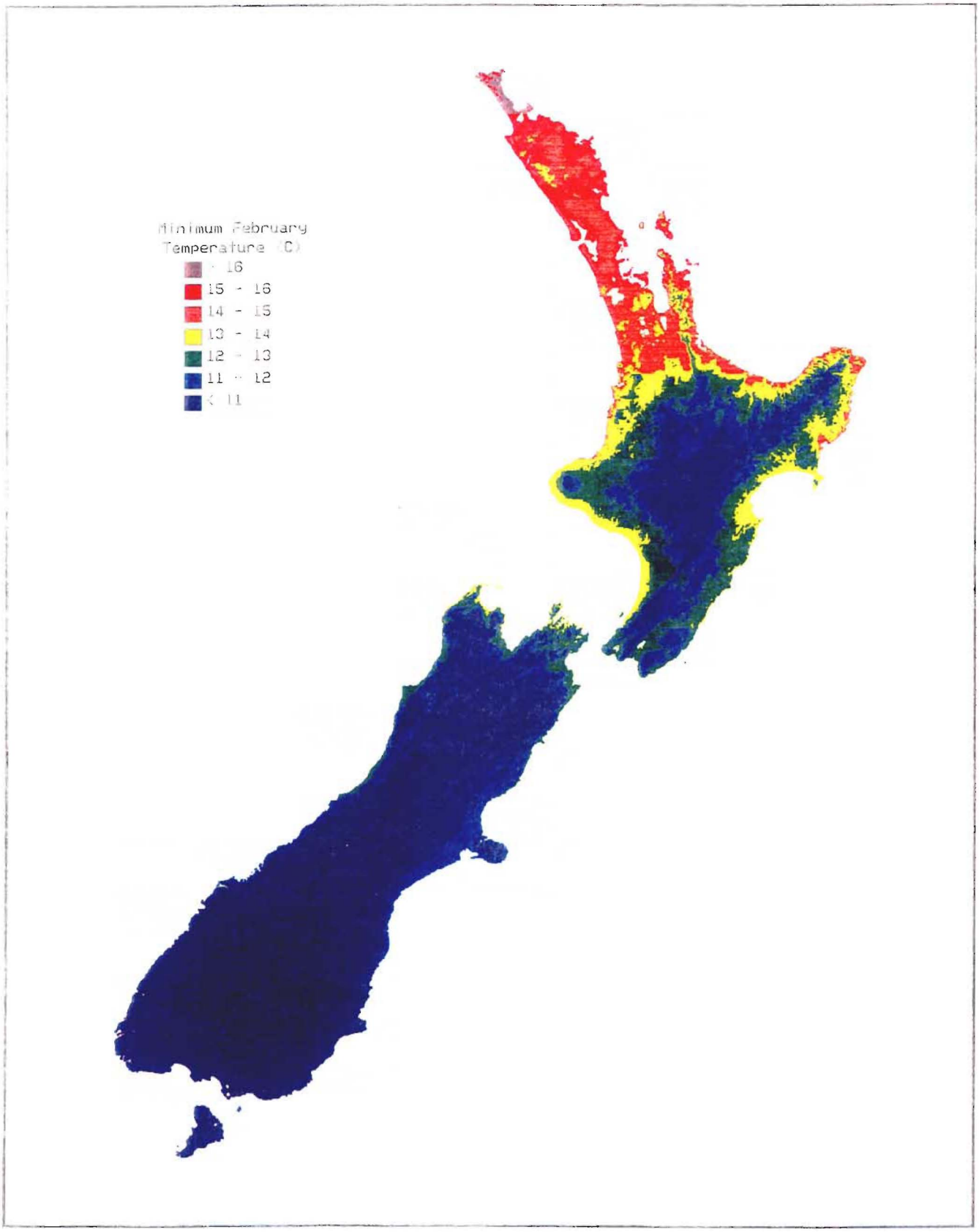

Figure 5.7

A map of the mean daily minimum February temperatures for New Zealand, using a GIS mapping system.

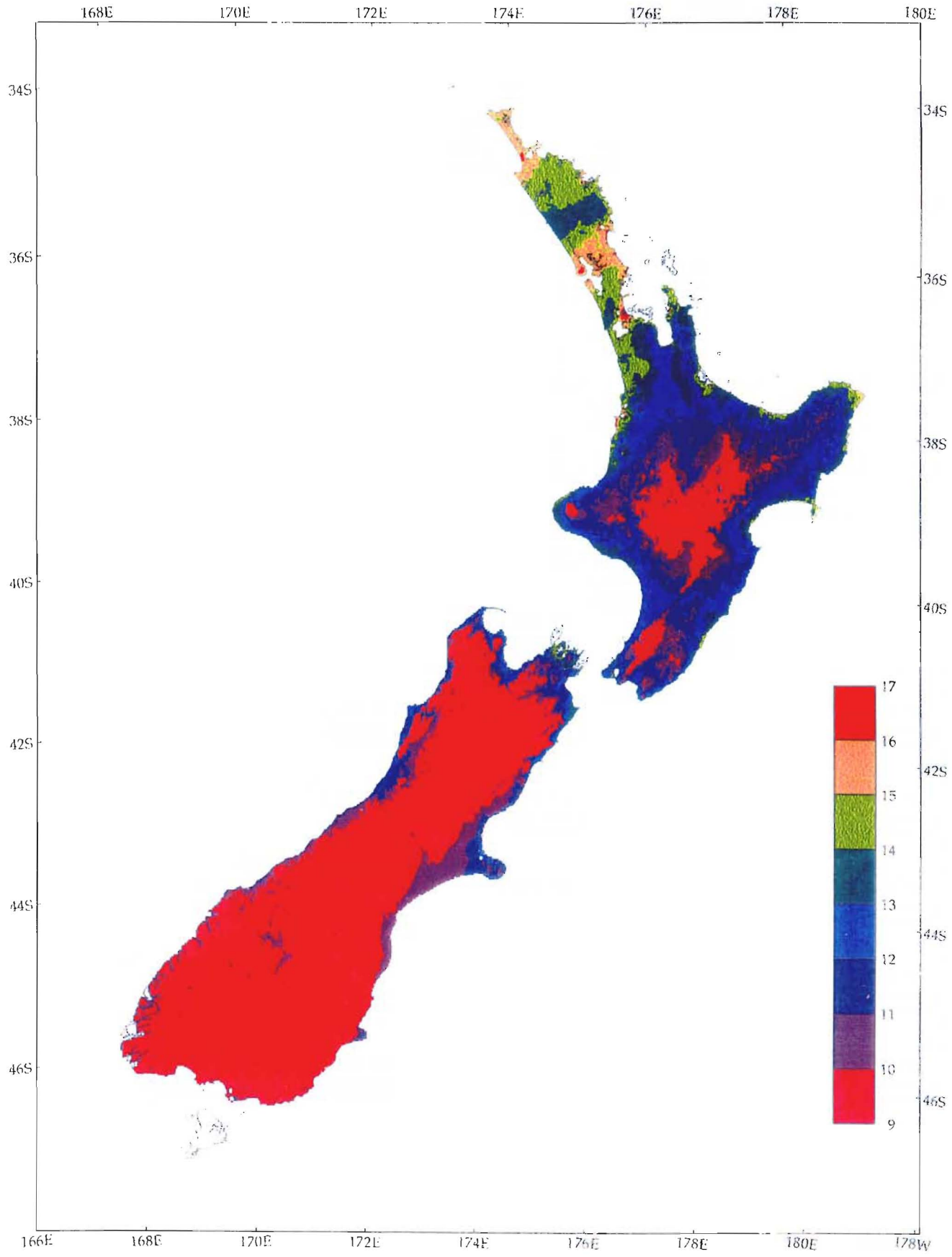

Figure 5.8

A map of the mean daily minimum February temperatures for New Zealand, using the Mitchell climate surface model.

D. DISCUSSION

In the 1994 validation, strobilus production was again found to favour sites that had warmer February temperatures, particularly those in the north of both island's.

As for the 1992 study there were significant ($p<0.0001$) differences between sites in counts of strobili. This further indicates that the associated error of the sampling methodology was sufficiently small to allow between site-differences to be obtained.

1. Validation of the 1992 Model

Across the 12 eastern South Island sites, it was found that there was close general agreement between observed and predicted values. There were, however, 3 sites where the discrepancy was reasonably great. On 2 of those sites the estimated numbers were higher than the actual; and on the third site the actual number of strobili was higher than predicted. There are a number of possible explanations for these discrepancies.

Firstly, considering that the 1992 model was only able to explain 65% of the variability in strobilus production between sites, it was not expected that all predictions in 1994 would be in close agreement with actual values. However, it is also likely that there may be some specific site by year interactions in strobilus production.

One factor which is suspected to be involved on some sites where actual counts are less than predicted is opossum browsing. Opossums are known to feed on both male and female strobili at the time of anthesis; and their populations vary according to the intensity of control measures applied in different regions at different times. Substantial year-to-year variability can occur. Other specific factors such as wind damage may also reduce strobilus numbers selectively on some sites.

It is less easy to explain the cause when strobilus production on a site greatly exceeds that predicted by the model. Hanmer-2 was the major example of this with 27.6 strobili in 1994 compared with the predicted value of 8.7. Whether that actual count reflects a genetic effect, or a microsite effect, or the effect of a particularly favourable year is not known. But it is known that a stand in Hanmer near to that assessed in 1994 had 3.3 strobili in 1992; a value very

close to the predicted one.

When the model was used to estimate strobilus numbers in the North Island, where it had not been developed, the errors increased. For the warmer North island sites, the counts of strobili estimated by the model were considerably above the actual counts. As indicated earlier, one would expect a biologically-based model such as this not to remain linear over an extended temperature range. The over-estimation in the north of the North Island indicated that a more complex function was likely to fit better than the linear function used to date.

2. Revised Model - Combined 1992 and 1994 Database

Following the validation of the 1992 model in the South Island and the North Island it was considered appropriate to re-model strobilus counts across the whole country and establish whether the multiple regression analysis re-selected the same climatic and soil variables into a new model equation. Thus the 1992 and 1994 databases were combined. Again February mean minimum temperature, G_f and May minimum temperature were found to be significantly correlated with strobilus counts, in that order of importance; as was long term February temperature. Accordingly, when strobilus counts were re-modelled a similar model was constructed to the preceding 1992 model, and explained around 62% of between-site variance.

The soil water stress variable which accounted for 6% of the variance of the South Island model, became non-significant when the data from the country as a whole was modelled. This does not necessarily indicate that soil water stress is unimportant to the strobilus initiation/differentiation process. It is clearly of much less importance than temperature, but the opening up of the database to both west and east coast sites in the North Island may have reduced its statistical significance. Along the east coast of the South Island in 1992, however, water stress was found to account for a significant part of the variance, albeit only 6% (see Chapter 4).

The February temperature variable appeared to be a sound predictor of strobilus counts, and from the regression analysis there appears little doubt that site temperature during the time of seed-cone bud differentiation has an important influence on the number of emergent strobili. To confirm that during February seed-cone bud differentiation was occurring across all sites, terminal buds were collected while counting strobili in 1994 for the validations. They were dissected to establish the presence or absence of long shoot primordia. There were only three

of the 22 sites where initiated primordia were not present in buds, and these were the sites of lowest numbers of strobili. Those results indicated that generally, reasonably irrespective of site location, axillary primordia are developing in February. It thus seems likely that the correlations with February temperature may be regarded as a direct impact on strobilus differentiation.

As indicated earlier, biological considerations made it unlikely that the relationship between climate and strobilus production would remain linear over New Zealand as a whole. There is a reasonable level of understanding of the impact of temperature on the vegetative growth of radiata pine, and an optimal day/night temperature of 20°C/5°C has been defined (Hellmers and Rook, 1973; Jackson and Gifford, 1974). But no such knowledge exists for reproductive behaviour. There is a publication by Lanner (1966) in which he reports that radiata pine at an altitude of 1550 metres in Hawaii produces receptive strobili over a 9 month period of the year. After obtaining some meteorological data for this site (Appendix F) it was possible to compare temperatures in Hawaii with those in North Auckland. Essentially the long term mean minimum temperature in August (the Northern Hemisphere equivalent of February) in Hawaii was some 5°C colder than the warmest sites in North Auckland. However, the annual range of mean monthly minimum temperatures was only 4.6°C, compared with 7°C for Kaitaia, for example, in the far north of New Zealand. The implications of this for the size of the strobilus crop at anthesis are discussed later in Chapter 8.

Lanner's paper is not in any sense quantitative. It was thus felt necessary to explore whether a non-linear relationship would provide a better fit for the model than a linear one.

Planning to improve the fit, however, raised another issue of ease of use of the model. The model which had been developed from the 1992 data, and extended with the 1994 data contained inputs which were not readily obtainable by a manager looking for an orchard site. Firstly it was based on climatic data which applied specifically to a given year's strobilus counts; but secondly some of the climatic parameters were not routinely recorded by any organisation. They would need to be collected personally, and at a specific time of the year. It was that consideration that led to the concept of simplifying the model so that it was usable more broadly across New Zealand as a predictive tool.

3. The Schumacher Equation

Because mean minimum February temperature data has been collected from a wide range of meteorological stations in New Zealand over more than 30 years, and because it was a component of both the GIS mapping system (Barringer, 1995) and the Mitchell climate surface model (Mitchell, 1991) it was a logical climatic parameter to use. And as a predictor of strobilus number across sites, it explained only 2% less of the variability than did mean minimum February temperature for the specific year in which strobili were counted.

The possibility that a non-linear function would provide a better model fit to the February temperature and strobilus data was explored, to some extent. Plots of the residuals of the preceding linear models indicated that their appropriateness depended on $\log_e$-transformation of the strobilus data, in an attempt to meet regression assumptions. Considering that this form of transformation was best suited for the data supported the suggestion that a non-linear model may be more suited to predicting counts across all sites.

The Schumacher growth function fitted the data satisfactorily. While it had the advantage of reducing the level of over-prediction of the linear model at the high temperature end, it was still not a biologically satisfactory model in that there were insufficient data points at the high temperature end of the range to produce the sigmoid-shaped curve which might be expected. It is clear from the residual plot that the model now tends to over-predict at the low-temperature end and under predict at the high temperature end, and has an element of under-prediction for the mid-range temperatures. The low-temperature end is not important in terms of seed orchard siting, but if the model is to be refined in the future, collection of data from the warmer parts of New Zealand will be important.

4. Site Predictions - Using a GIS Mapping System and The Mitchell Climate Surface Model

One advantage of using a readily available predictor of strobilus production such as mean minimum February temperature is that it is readily calculated and mapped using both a GIS system and the Mitchell climate surface model. The printout of two maps of mean minimum February temperature for New Zealand each of which can be used to predict strobilus production capacity broadly across the country (Figures 5.7 and 5.8) are expected to be particularly helpful to seed orchard managers.

The maps that were generated indicated that the sites most likely to produce high numbers of strobili are in the north of New Zealand, and have oceanic as distinct from semi-continental climates. Perusal of the maps indicated that this is a likely reason why the multiple regression analysis selected mean minimum February temperature into the model equation rather than for example, mean February temperature or mean maximum February temperature. Selection of the latter variable would have included some of the more continental parts of New Zealand which do not yield high numbers of strobili.

CHAPTER 6

CORRELATIONS OF NUMBERS OF EMERGENT STROBILI WITH OTHER TREE PARAMETERS

A. INTRODUCTION

So far the only material reported from the survey of 52 sites east of the Main Divide has been the numbers of emergent strobili, reported in Chapter 4. That parameter was selected as the key one to be modelled as, despite a recognition that strobilus initiation is merely the first step towards seed production, it is the key step. If strobilus initiation is poor, it is immaterial whether or not subsequent seed yields per cone are high.

However, now that the capacity exists to predict sites with a high yield of strobili, it is necessary to determine how satisfactory these sites are likely to be in terms of a number of other relevant parameters for each of the 52 sites. In this chapter, data will be presented on the following parameters: mean tree height, percentage of trees bearing emergent strobili, incidence of abortion of strobili 4 months after anthesis, mean numbers of seeds per cone, and seed weight. In addition, the mean numbers of strobili per site reported in Chapter 4, will be broken down into first cycle strobili, and those in later cycles.

Bearing in mind that the overall objective of the thesis is to assist seed orchard managers to identify sites which are optimal for their needs, the initial approach adopted in this chapter will be to correlate these other parameters with total strobilus production.

B. MATERIALS AND METHODS

1. Tree Measurements

During October 1992 when counts of strobili were being made, individual tree heights were recorded at each site (n=40). Measurements where made using a "Suunto" clinometer (see Chapter 3).

2. Cone Collection

At each site in October 1992, recently matured cones were collected at random from 10 of the 40 trees on which strobilus counts were made. 1 cone was collected per tree (n=10). From each cone, seed was extracted (following kilning as per Warren and Fordham, 1978), cleaned, counted and weighed. The mean number of full seeds per cone and 1000-seed weight was calculated for each site.

3. Analysis of strobili

At each site in October 1992, counts of the total number of emergent strobili on each tree were recorded separately by annual growth cycle. In this chapter, the mean number of strobili per site which were present in the first annual growth cycle are presented. Similarly, from the data collected in 1992, the percentage of the 40 trees per site that carried emergent strobili was calculated and is presented here.

4. Conelet Abortion Assessments

During February 1993, the 40 trees per site on which the strobilus counts had been made in October, 1992 were re-visited, and the strobili in the top 2 metres of crown were re-counted. The data were expressed as percentage abortion from October to February. Previous research (Sweet and Thulin, 1969) has shown clearly that, by 3 months after pollination, 90% of the total abortion which will occur at a site has taken place. Because there had been significant needle growth on the trees between October and February, it was less easy to count strobili from the ground on the second date, and it is possible that some were missed. Any error, however, should have been consistent across sites.

5. Statistical Analysis

All statistical analyses were completed using the SAS statistical package (SAS Institute, 1987).

Counts of emergent strobili were correlated with several variables, including tree vegetative and reproductive parameters (as outlined above), by Pearson's correlation coefficient, using the PROC CORR procedure (SAS Institute, 1987). The normality of the data was tested using the PROC UNIVARIATE procedure (SAS Institute, 1987). Skewed data were $\log_e$-transformed to satisfy regression assumptions (Finney, 1973). As a further step to check on the appropriateness of the simple correlation coefficients Spearman's Rank correlation coefficients, which are nonparametric, were also calculated using the PROC CORR procedure (SAS Institute, 1987).

Variance quoted in the text is ±SE, unless stated otherwise.

C. RESULTS

1. Numbers of First Cycle Strobili

Differences between sites in this parameter ranged from 0 to 24.75. They were significant at the 0.0001 level. The mean productivity of the top 10 sites (18.50) was more than double the mean of all sites 8.60±1.12 (Table 6.2).

The 1992 data for mean total number of emergent strobili counted across sites was highly correlated (r =0.94) with the mean total number of strobili produced in the *first* annual cycle of growth (Table 6.1). That is, sites which bear high numbers of emerging strobili in total, also bear high numbers in the first cycle of the annual shoot. Thus the correlations with climate developed for total strobili in Chapter 4 also apply to first-cycle strobili.

In fact a very high proportion of the total strobili across sites was from first cycle strobili. The mean site had 9.6 strobili in total, of which 91% were from the first annual growth cycle. On the most productive 10 sites, however, 2nd and 3rd cycle strobili were more important, with the mean number of strobili being 21.8, of which 84% were from the first cycle.

Again the stepwise multiple regression analysis (see Chapter 4) selected mean minimum February temperature, soil water stress integral and G_f as significant independent variables (see Table 6.3). Although of little relevance, this time soil water stress was selected ahead of G_f: in Chapter 4 the reverse situation ocurred. The May variable was only significant at the 10% level. The overall coefficient of determination (r^2) of the model was 0.65. The February variable accounted for around 54% of between-site variance in strobilus counts.

2. Variability in the number of trees producing strobili

The data are presented in Table 6.4. On the mean of 52 sites, 81% of the trees carried emergent strobili, but on the most productive 10 sites, 98% carried strobili. Thus the more productive the site, the higher the percentage of trees carrying strobili. On the poorest sites around 30% of the trees only, carried strobili.

Across sites, the correlation between the percentage of trees that produced emergent strobili and the mean total counts of emergent strobili was 0.87, significant at the 0.0001 level.(Table 6.1).

3. Conelet Abortion

Across all sites the percentage of strobili lost through abortion ranged from 6% - 64% with a mean of 37±5% (see Table 6.4). These differences were significant at the 0.0001 level. There was no correlation between abortion level and total numbers of emergent strobili (r= -0.05 - see Table 6.1). The top ten sites for strobilus production had a similar level of conelet abortion to the overall mean for the 52 sites. There was no readily apparent relationship of abortion levels to site or climate.

4. Seed Yield per Cone.

The mean number of seeds per cone was 113±13.1, with values for individual sites ranging from 44 to 147. Differences between sites were significant at the 0.0001 level (see Table 6.3). Across sites (see Table 6.1), the number of seeds per cone was significantly correlated with the number of emergent strobili (r=0.48, significant at 0.0004%). In other words, highly productive sites, in strobilus terms, were in general sites with high seed yields per cone, although the relationship only explained 23% of the variability. There were 5 sites where the mean seed yield per cone exceeded 140. All of these were in fact Canterbury sites, but not all Canterbury sites had high seed yields per cone.

5. Seed weight

Mean 1000-seed weights ranged across sites from 21.3g to 41.5g, with a mean of 32.1±2.35g. Site differences differed significantly at the 0.0001% level. There was no correlation between productivity of a site in terms of numbers of emergent strobili and 1000-seed weight (r=0.26 - not significant). The 10 most productive sites in terms of strobilus number had seed which were very similar in weight to the mean of all sites. The 1000-seed weight was significantly ($p<0.0001$) correlated with the number of full seeds per cone ($r = 0.63$).

6. Tree Height

Mean data for each site are presented in Table 6.5. The data are highly statistically ($p<0.0001$) significant across sites; the mean value was 10.11±0.24m. Table 6.1 shows that across sites there was a significant correlation between tree size and numbers of emergent strobili. The correlation was not a particularly high one, however, with tree height explaining only 23% of the variability in strobilus number.

Table 6.1

Correlations (r) of mean total numbers of emergent strobili with other tree, bud and seed parameters, recorded across sites. The level of significance (Pr>F) of each correlation is shown in parenthesis.

Variable	Numbers of emergent strobili r
[1] Number of emergent strobili/first cycle	0.94 (0.0001)
[1] Percentage trees carrying strobili	0.87 (0.0001)
[1] Tree Height (m)	0.48 (0.0022)
[1] Abortion (%)	-0.05 (0.7144)
[2] Full seed number/cone	0.48 (0.0004)
[2] 1000-seed weight (g)	0.26 (0.0701)

[1] Data for variable collected in 1992 survey study - across 52 sites along the eastern side of the South Island.

[2] Data for variable collected in 1992 study - across 50 sites as cones were only collected from 1 of the sites at Waimate, and no cones were able to be found at the Low Mount stand.

Table 6.2

Mean numbers of emergent strobili in the first annual cycle of shoot growth across eastern South Island sites. Counts were made in October 1992; on trees aged between 10 and 12 years. At each site the number of first cycle strobili in the top 2 metres of crown of 40 trees was counted. The data presented are means per tree.

No	Site - 1992	Mean total number emergent strobili	Mean number strobili (first cycle)	Standard error (first cycle)
1	Rabbit Island	31.9	24.7	2.58
2	Motueka	28.4	22.2	2.03
3	Appleby	24.2	18.6	2.21
4	Grassmere	20.1	18.1	2.07
5	Kaikoura	19.8	19.2	1.31
6	McLeans	19.7	18.7	2.12
7	North Bank	19.6	15.7	1.49
8	Makikihi	19.3	17.7	1.75
9	Mayfield	18.5	15.8	1.76
10	Birch Hill	16.9	14.3	1.62
11	Ashley Forest	16.1	15.1	1.77
12	Blenheim	15.0	13.1	1.99
13	Woodend	14.6	13.6	1.48
14	Moeraki Boulders	14.0	13.3	1.12
15	Waimate-10	12.6	11.7	1.57
16	Salt Water Creek	12.4	12.2	1.65
17	Rakaia	11.5	10.5	1.14
18	Awatere Valley	11.5	9.9	1.33
19	Spotswood	10.3	9.1	1.77
20	Oamaru	10.1	10.0	1.40
21	Wairau Valley	10.0	8.6	1.25
22	Rangitata	10.0	9.3	1.39
23	Waimate-12	9.5	8.9	1.47
24	Argyle	9.3	8.6	1.19
25	Winchmore	9.0	8.4	0.97
26	Lincoln	8.3	8.2	1.05
27	Rangiora Nursery	7.9	7.2	1.10

28	Kurow	6.5	6.1	1.02
29	Spencerville	6.4	5.7	0.86
30	Lake Waihola	5.9	5.6	0.89
31	Merivale Station	5.4	4.9	0.65
32	Orari	5.2	4.8	0.86
33	Amberley Beach	5.1	4.9	1.35
34	Homebush	5.0	4.8	0.86
35	Amberley	4.8	4.3	0.69
36	Tapanui	4.7	4.6	0.86
37	Darfield	4.6	4.3	0.88
38	Cromwell	4.5	4.2	0.63
39	Balmoral	4.1	3.7	0.62
40	Eyrewell - Wrights	3.9	3.7	0.53
41	Burkes Pass	3.8	3.7	0.80
42	Wanaka	3.7	3.2	0.77
43	Hanmer	3.3	3.2	0.41
44	Eyrewell - Downs	3.1	2.9	0.46
45	Dunsandel	2.9	2.8	0.68
46	Crown Range	1.8	1.7	0.38
47	Dunback	1.6	1.5	0.41
48	Dunedin	1.2	1.2	0.42
49	Tara Hills	1.2	1.1	0.25
50	Glynn Wye	1.1	1.1	0.31
51	Hororata - West	0.9	0.9	0.38
52	Low Mount	0.0	0.0	0.00
	Pr>F (site)	0.0001	0.0001	
	Mean of top 10 sites	21.84	18.50	
	Mean of 52 sites	9.63	8.60	
	Range of 52 sites	0 - 31.9	0 - 24.7	

Table 6.3

The four variables listed accounted for around 65% of the overall variation of Y about its mean value. The regression coefficients, together with their standard errors, are listed. The level of significance (Pr>F) of each variable is shown in parenthesis.

Variable	Coefficient	S.E.
Feb. temp.	0.134 (0.0114)	0.050
S_ψ	-0.009 (0.0095)	0.003
G_r	0.002 (0.0098)	0.001
May temp.	0.009 (0.1082)	0.060
Intercept term	-0.0729	

The corresponding equation may be written as follows:

$$\log_e(\text{strob}) = 0.134\,(\text{Feb temp}) + 0.002\,(G_r) - 0.009\,(S_\psi) + 0.009\,(\text{May temp}) - 0.073$$

The variables have the following meaning:

$\log_e$(strob) - number of emergent strobili ($\log_e$-transformed to satisfy regression assumptions)

Feb temp. - mean minimum temperature (°C) for February 1992.

G_r - accumulated growing degree days (base 10°C) from August 1991 to November 1991 weighted against rainfall for those months.

S_ψ - soil water stress integral (-MPa) for February 1992 and March 1992.

May temp. - mean minimum temperature (°C) for May 1992.

Table 6.4

Counts of strobilus and seed data - 1992 survey study. Counts of strobili were made during October 1992; on trees aged between 10 and 12 years. At each site the number of strobili in the top 2 metres of crown of each of 40 trees was counted. At each site 10 cones were collected at random, 1 per tree. Abortion assessments were made during February 1993. The data are presented as mean values.

No	Site	Mean number strobili - 1992	% 40 trees carrying strobili	Abortion (1993) (%)	[1]Full seed number per cone	[1]1000-seed weight (g)
1	Rabbit Island	31.9	100	26.9	119.9	36.5
2	Motueka	28.4	100	33.3	123.6	26.4
3	Appleby	24.2	100	22.2	129.4	21.3
4	Grassmere	20.1	100	52.8	136.1	29.1
5	Kaikoura	19.8	100	56.8	124.0	36.1
6	McLeans	19.7	93	30.6	145.5	39.2
7	North Bank	19.6	100	26.7	113.4	30.5
8	Makikihi	19.3	97	53.9	138.3	33.1
9	Mayfield	18.5	100	41.2	138.8	41.5
10	Birch Hill	16.9	95	59.6	135.0	36.1
11	Ashley Forest	16.1	92	49.5	113.0	34.7
12	Blenheim	15.0	97	42.7	122.0	28.8
13	Woodend	14.6	95	30.5	143.0	37.4
14	Moeraki Boulders	14.0	100	49.2	126.2	31.7
15	Waimate-10	12.6	97	47.0	128.0	30.9
16	Salt Water Creek	12.4	92	30.1	124.7	35.1
17	Rakaia	11.5	95	26.7	146.8	35.4
18	Awatere Valley	11.5	95	43.8	128.0	41.1
19	Spotswood	10.3	84	64.1	114.4	29.3
20	Oamaru	10.1	95	39.1	114.0	35.2
21	Wairau Valley	10.0	90	21.5	102.0	32.7
22	Rangitata	10.0	80	36.9	108.5	33.1
23	Waimate-12	9.5	92	33.0	n/a	n/a
24	Argyle	9.3	90	29.8	121.4	31.9
25	Winchmore	9.0	92	26.3	116.3	30.4
26	Lincoln	8.3	90	41.5	96.0	32.8
27	Rangiora Nursery	7.9	87	51.6	136.0	39.5

28	Kurow	6.5	82	24.8	101.5	32.8
29	Spencerville	6.4	92	24.1	138.8	29.6
30	Lake Waihola	5.9	80	64.9	133.7	29.5
31	Merivale Station	5.4	82	20.5	68.4	32.0
32	Orari	5.2	72	42.4	43.7	30.0
33	Amberley Beach	5.1	75	14.3	100.4	29.2
34	Homebush	5.0	95	27.1	87.4	35.1
35	Amberley	4.8	77	31.3	126.8	36.8
36	Tapanui	4.7	85	42.7	113.7	29.0
37	Darfield	4.6	70	36.2	92.4	29.9
38	Cromwell	4.5	77	42.7	75.5	31.7
39	Balmoral	4.1	75	49.0	102.6	38.6
40	Eyrewell - Wrights	3.9	82	39.0	114.2	31.0
41	Burkes Pass	3.8	64	43.7	58.0	29.1
42	Wanaka	3.7	87	34.2	129.2	30.1
43	Hanmer	3.3	80	22.9	104.0	27.9
44	Eyrewell - Downs	3.1	87	28.4	147.4	35.2
45	Dunsandel	2.9	92	42.7	146.9	33.2
46	Crown Range	1.8	50	53.6	106.2	30.8
47	Dunback	1.6	47	46.9	93.3	31.6
48	Dunedin	1.2	27	27.2	76.0	24.8
49	Tara Hills	1.2	30	39.5	68.4	24.0
50	Glynn Wye	1.1	30	6.5	85.7	23.9
51	Hororata - West	0.9	30	62.3	108.6	32.4
52	Low Mount	0.0	0	0.0	n/a	n/a
Pr>F (site)		0.0001	0.0001	0.0001	0.0001	0.0001
Mean first 10 sites		21.84	98.5	40.4	130.4	32.9
Mean all sites		9.63	81.0	37.1	[1]113.0	[1]32.1
Range of all sites		0 - 31.9	0 -100	6 - 64	44 - 147	21.3 - 41.5

[1]Only 50 sites were sampled for these variables as cones were collected from only 1 site at Waimate, and no cones were able to be found at the Low Mount stand.

Table 6.5

Numbers of emergent strobili in the first annual cycle of growth and tree height across eastern South Island sites. The data were collected in October 1992 and are presented as means per tree.

No	Site	Mean total number emergent strobili	Tree height (m)
1	Rabbit Island	31.9	12.2
2	Motueka	28.4	11.8
3	Appleby	24.2	11.5
4	Grassmere	20.1	10.5
5	Kaikoura	19.8	11.8
6	McLeans	19.7	9.3
7	North Bank	19.6	15.4
8	Makikihi	19.3	9.4
9	Mayfield	18.5	10.6
10	Birch Hill	16.9	13.2
11	Ashley Forest	16.1	10.4
12	Blenheim	15.0	10.6
13	Woodend	14.6	11.3
14	Moeraki Boulders	14.0	11.6
15	Waimate-10	12.6	8.6
16	Salt Water Creek	12.4	8.8
17	Rakaia	11.5	8.4
18	Awatere Valley	11.5	10.0
19	Spotswood	10.3	9.1
20	Oamaru	10.1	11.4
21	Wairau Valley	10.0	7.2
22	Rangitata	10.0	11.3
23	Waimate-12	9.5	11.7
24	Argyle	9.3	13.5
25	Winchmore	9.0	11.9
26	Lincoln	8.3	10.6
27	Rangiora Nursery	7.9	9.9

28	Kurow	6.5	10.7
29	Spencerville	6.4	11.7
30	Lake Waihola	5.9	8.3
31	Merivale Station	5.4	8.7
32	Orari	5.2	9.2
33	Amberley Beach	5.1	9.8
34	Homebush	5.0	9.0
35	Amberley	4.8	9.8
36	Tapanui	4.7	11.6
37	Darfield	4.6	10.4
38	Cromwell	4.5	9.5
39	Balmoral	4.1	9.4
40	Eyrewell - Wrights	3.9	16.9
41	Burkes Pass	3.8	9.2
42	Wanaka	3.7	8.2
43	Hanmer	3.3	9.6
44	Eyrewell - Downs	3.1	9.2
45	Dunsandel	2.9	8.7
46	Crown Range	1.8	11.7
47	Dunback	1.6	6.1
48	Dunedin	1.2	10.9
49	Tara Hills	1.2	6.1
50	Glynn Wye	1.1	9.5
51	Hororata - West	0.9	5.5
52	Low Mount	0.0	4.5
Pr>F (site)		0.0001	0.0001
Mean of first 10 sites		21.84	11.57
Mean of 52 sites		9.63	10.11
Range of 52 sites		0-31.9	4.5-16.9

D. DISCUSSION

The intent of this study was to assess attributes other than numbers of emergent strobili that were important to the selection of seed orchard sites. And then to explore whether or not they were independent of numbers of strobili produced. A further aspect was to establish whether sites that produced the greatest numbers of strobili did this by producing several cycles of strobili in the annual shoot as opposed to having more sites in the crown which bore first-cycle strobili.

1. First or Single Cycle Strobili

The results showed a very high correlation across sites between total emergent strobili, and those produced in the first seasonal growth cycle. That implies that the model presented in Chapter 4 would appear very similar had it been constructed using first cycle strobili only. Indeed this was found to be the case when first cycle strobili were modelled.

The issue of the model being able to predict single cycle strobili is seen as a potentially important one for selection of sites for meadow orchards because, owing to the small size of meadow orchard ramets, they possibly produce multiple cycles of annual shoot growth less often than do trees of the size that were assessed in this experiment.

2. Conelet Abortion

Conelet abortion is a problem in seed orchards which has attracted significant amounts of research over a time period of more than 20 years. Although some understanding of its physiology and causes exists (Sweet and Thulin, 1969), it has not proved possible for orchard managers to reduce its impact significantly on a routine basis. It is thus very important in selecting sites for seed orchards, to have some knowledge of abortion levels.

This thesis was not seriously targeted at abortion, but it was thought important to determine whether conelet abortion was related to strobilus productivity; or whether it was independent of this. The mean value across all sites of 37% of the strobili which were present in October 1992 being missing in February 1993 is of the order that would be expected from the literature. Sweet (1975) reports an average figure of 40%abortion across a large number of pine species. In radiata pine seed orchards, average values of around 40% are common (NZ Seed Orchard

Research Group, pers. comm. 1992): this study however, is the first known to have explored the phenomenon in forest stands for radiata pine.

As known from previous seed orchard studies, the impact of site on abortion is very striking, with a range in this study from 6% to 64%. Correlation analysis however, showed this to be un-related to strobilus productivity. Until the relationship between abortion, and site and climatic factors can be modelled (and the data collected here would allow that to be done), it will be necessary for seed orchard managers, in choosing orchard sites, to obtain their own data on this parameter, and use it in comparing competing sites.

The reason(s) for variation across sites in abortion levels is largely unclear. It is likely that there are a number of contributing factors, not all of which may be primarily climate-based. The extent to which a climate-based model could explain the variability in abortion would in itself provide helpful information to seed orchard managers.

3. Percentage of Trees Bearing Emergent Strobili

Interest in this parameter relates again to the selection of orchard sites. The evidence from the analysis is that 75% of the variability in total strobilus production across sites is associated with variability in the percentage of trees carrying strobili. That relationship offers a powerful diagnostic tool to a manager looking for an indication of the strobilus bearing potential of a site. The higher the proportion of trees that carry strobili, the better the potential of the site.

4. Yield of Full Seeds Per Cone

Again, an orchard site which does not produce high numbers of sound seeds per cone is a problem. The variability in this parameter was high, and only some 23% of this was correlated with total strobilus production. The data set could offer the opportunity to look for relationships between full seeds per cone and site and climate, and that would be a valuable future exercise. In the interim, the data provide the manager with a spectrum of values within which to evaluate any prospective seed orchard site.

5. Seed Weight

Again, the data showed considerable site variation in this parameter. It appeared to be quite unrelated to the level of strobilus production across sites. Seed size is regarded as an important parameter (Griffin, 1972; Clair and Adams, 1991), and once again, the data presented here provide a picture of the variability which exists, and an opportunity to evaluate the seed size on any prospective site.

A significant correlation was found (r=0.63) between full seed number per cone and 1000-seed weight. Thus although the correlation between strobilus number and seed weight is relatively weak an analysis of the number of full seeds per cone at a site may give some indication as to the likely size of seed it will produce.

6. Tree Height

Variability in tree size across sites is always an issue in a study such as this where it is not possible to match tree age or size exactly. The approach adopted in this study was to count strobili only in the top 2 metres of crown in each tree. Preliminary assessment indicated that on trees aged between 10 and 12 years, this assessment was relatively independent of tree size (see Chapter 3). However, the data reported in this chapter indicate that there was a correlation, albeit one which explained only 23% of the variability in strobilus production in terms of tree height.

Whether the relationship is a primary causal one is arguable. A positive correlation between temperature and strobilus production was well established in Chapter 4. The literature would also indicate a positive correlation between temperature and tree growth over the general area which was sampled here (Jackson and Gifford, 1974). Thus there is no reason *per se* to see tree size as having confounded the climatic relationships obtained. Having said that, however, the relationship between crown size and number of branches suited to bearing strobili, which has also been implied in the model, should not be overlooked.

To summarise, having used the model in Chapter 4 to ascertain the broad general areas which are favourable for strobilus production, the orchard manager then needs to use existing stands close to potential orchard sites to check on other parameters. The data in this chapter suggest that desirable values might be:

1. The percentage of trees carrying emergent strobili should be more than 90%.

2. The percentage of abortion of strobili 4 months after anthesis: Positive values would be below 30%.

3. The number of full seeds per cone should ideally exceed120.

4. The weight of 1000 seeds should ideally exceed 35 g.

It is of interest that only 1 of the top 10 sites for strobilus production (Rabbit Island) comes close to matching all of these criteria. All of the others are less than optimal in at least one criterion.

As a whole, the information presented in this chapter is a necessary adjunct to the material presented in Chapters 4 and 5. Assessment of the variables discussed in this chapter would provide important additional data for the selection of potential seed orchard sites.

CHAPTER 7

TIMING OF ENVIRONMENTAL TREATMENTS FOR STROBILUS INDUCTION

A. INTRODUCTION

A major part of the plan for the research reported in this thesis was to carry out experimental studies. Because of the time constraints of Ph.D. research, it was not possible to develop the strobilus production model reported in Chapter 4, and **then** test it experimentally. Neither was there of course any certainty at the start that the work in Chapter 4 would even result in a clear outcome.

The experimental studies were carried out over 2 years, 1993 and 1994. Because they were conducted in parallel with the model development, the first year's experiments (designed in December, 1992) were designed with no knowledge of the likely outcome of the modelling exercise. Thus the parameters examined were based solely on an analysis of the literature, and on personal perceptions as to which environmental factors might be important.

By the start of the second year's experiments (planned in December, 1993) there was preliminary information from the modelling exercise that temperature may become a more important variable than water stress; but the model itself was not completed until December, 1994, well after all the experimental work had been completed.

Thus, although the experimental chapters are presented in this thesis **after** those relating to the development of the model, it is important to confirm that this does not represent the time sequence in which the work was done. The experiments need to be seen, not as a verification of the model, but as a set of independent attempts to determine the climatic parameters affecting strobilus initiation.

Before one applies treatments to influence the initiation/differentiation of strobili, it is critical to have a clear understanding of the timing at which the process is affected by environmental factors. Information, at the time these experiments commenced, came from 2 sources. The first

was the morphological studies of Bollmann and Sweet (1976;1979). These established, for a number of clones in the central North Island that initiation of long shoot primordia occurred in mid-December, with the first microscopically-recognisable differentiation into strobili occurring 6 weeks later, at the end of January. That study has not been repeated in Canterbury, but the bud dissections reported in Chapter 3, showed clearly recognisable seed cone buds on the 12th of March, 1992. That result suggests that the timing is not too different from the central North Island. This was further supported by the bud dissection data in the validation study (see Chapter 5) which indicated that long shoot primordia had been initiated by February at all South Island sites, apart from two south of Amberley.

The second source of information was a number of experiments carried out at Amberley seed orchard which explored the optimal timing of gibberellin $A_{4/7}$ application, in terms of its effect on strobilus number. On the basis of effectiveness, gibberellin application has traditionally been carried out during February; but recently detailed studies by Siregar (1994) confirmed the period from the 17th to the 25th of February as being the application time which gave the optimal response in increasing strobilus number.

Sweet (1979) demonstrated that when $GA_{4/7}$ was applied to buds in which long shoots had already been initiated, its action was to increase the total number of long shoots differentiating and the direction in which they developed. Application prior to long shoot initiation has not been effective. One of the questions arising, however, concerns the issue of whether environmental and chemical stimuli influence the same developmental stages of the buds.

An impact of ramet size on the timing of long shoot primordia initiation was reported soon after the undertaking of the research work in this chapter, by Dickson, Riding and Sweet (1994) (see Appendix A).

The development of the model in Chapter 4, identified mean minimum temperature in February as the single environmental factor most closely correlated with strobilus number across a number of sites. But the high level of intercorrelation of temperature data in different months does not lend confidence to the fact that February is the key time when environmental stimuli influence strobilus number. Thus, prior to applying environmental treatments aimed at increasing strobilus number, it was felt necessary to experimentally explore the time when environmental stimuli did impact on strobilus number.

This chapter thus reports 2 experiments aimed at establishing for Amberley seed orchard, the timing when seed-cone bud differentiation can be influenced. The next four chapters then consider the effects that air temperature, soil water status, spring growing conditions and nitrogen, respectively, had on strobilus numbers.

There are experimental studies in the literature that have changed the reproductive patterns of conifers by placing the date of seed-cone bud differentiation out of phase with the normal strobilus-forming stimulus; hence establishing the timing of the seed-cone differentiation along with the effect environmental conditions have on strobilus production (see Chapter 2). Larson (1961) showed that the strobilus bearing patterns of *Pinus banksiana* could be modified when the date of bud development was put out of synchrony with the normal environmental conditions of the growing season.

The intent of the experiments reported in this chapter was thus to use clonal material to explore the time at which external climatic factors influenced the numbers of emergent strobili at anthesis. The general time period incorporated in the experiment was that during which recently-initiated long-shoot primordia were determining the direction of their development.

Two experiments were conducted. In the first one, ramets were removed from the well-established reproductive environment of Amberley seed orchard to what was believed to be a non-strobilus forming environment. The timing and duration of removal was variable, and the intent was that this would provide information on times during which, if an appropriate environmental stimulus was not present, strobili would not form. The second experiment sought to build on and refine the results from the first.

B EXPERIMENTS

1. TRANSFER EXPERIMENT (Experiment 1)

1.1 MATERIALS AND METHODS

1.1.1 Site

This experiment, was carried out in 1993 at Amberley seed orchard.

1.1.2 Material

Potted grafts of three clones, all regarded as "reasonable flowerers" (Sweet, 1979), were used in this experiment.

In June 1992, following one year in the graft nursery, these grafts were lifted and potted up in "PB 95" planter bags; and grown for around 6 months before the 1993 experiment. The grafts in this experiment were in their first year after potting.

The growing medium used was a fine bark mix (MS55 - Oderings Nurseries (Wellington) Ltd) To ensure a base (sustainable) level of fertility, pots were fertilised with a general fertiliser mix ("Nitrophoska"). Pots were irrigated during the summer months whenever rainfall was seen as inadequate.

1.1.3 Gibberellin $A_{4/7}$ Application

Strobilus production in grafts one year after establishment at Amberley is relatively light. The average proportion of one-year-old grafts bearing strobili in the orchard is 41%, and a high figure for an early-bearing clone would be 70% (S.F. Van Ballekom, pers. comm.). Those values follow gibberellin application, without which strobilus productivity is considerably lower. For that reason, there was a prospect that strobilus initiation on one-year grafts would be inadequate for the experiment, unless gibberellins were used. To protect against that possibility, all grafts were treated with $GA_{4/7}$ on the 17th of February 1993. Each graft received a dose of 0.5mg of crystalline $GA_{4/7}$ in 95% ethanol, via a bud application. Both the dose rate and method of

application represent standard practice in New Zealand seed orchards for 1-year-old grafts.

1.1.4 Seed Extractory Shed

The "non-strobilus forming" environment used in this experiment was the cone-extractory shed at the seed orchard. It was believed that light intensity in the shed would be too low for strobili to initiate. Temperature and photosynthetically active radiation (PAR) were monitored in the shed.

1.1.5 Experimental Design

This experiment was conducted according to a 6×4×3 factorial design, namely 6 transfer times to the shed, 4 periods of time in the shed and 3 clones. There were 3 replicate grafts in each of the 72 treatment groups giving 216 grafts in the complete experiment. Grafts, in each of the clones, that were left continuously outside were regarded as controls.

During January, February and early March, grafts were moved into and out of the seed extractory shed as per the schedule given in Table 7.1.

Table 7.1

Schedule of graft transfers in one clone.

Schedule for one clone	Days held in shed			
	14 days	28 days	42 days	56 days
Date into shed	Date back to orchard			
1 Jan (12 grafts)	15 Jan (3 grafts)	29 Jan (3 grafts)	12 Feb (3 grafts)	26 Feb (3 grafts)
15 Jan. (12 Grafts)	29 Jan. (3 grafts)	12 Feb. (3 grafts)	26 Feb (3 grafts)	12 March (3 grafts)
29 Jan (12 Grafts)	12 Feb (3 grafts)	26 Feb (3 grafts)	12 March (3 grafts)	26 March (3 grafts)
12 Feb (12 Grafts)	26 Feb (3 grafts)	12 March (3 grafts)	26 March (3 grafts)	9 April (3 grafts)
26 Feb (12 Grafts)	12 March (3 grafts)	26 March (3 grafts)	9 April (3 grafts)	23 April (3 grafts)
12 March (12 grafts)	26 March (3 grafts)	9 April (3 grafts)	23 April (3 grafts)	7 May (3 grafts)

1.1.6 Light and Temperature Conditions Inside the Seed Extractory Shed

During the experiment, temperature and light were monitored in the shed using a CR10 Campbell data logger connected to a thermistor (for monitoring temperature) and a Licor quantum sensor (for monitoring light).

1.1.7 Assessments

By early May 1993, all grafts were again outside in the orchard, where they remained until September 1993, the time of anthesis. The numbers of (a) strobili, (b) branches and (c) latent buds produced in the first cycle, the only one that carried strobili on the grafts that year, were counted.

It was noted during the experiment, that conditions in the shed were such that grafts kept in for more than 4 weeks began to lose needles, and become chlorotic and stunted. Some grafts in fact died following long periods in the shed.

1.1.8 Statistical Analysis

Considering a significant proportion of grafts in this experiment did not carry strobili it was considered inappropriate to run a rigorous analysis of variance to test all main effects and interactions. None of the grafts held in the shed for longer then 42 days carried strobili and only a few grafts that were held for 28 days carried strobili. Thus only data for grafts (3 replicate grafts per treatment) in the 14 day treatment are presented along with ±SE.

1.2 RESULTS

1.2.1 Environmental conditions

These data are presented in Figure 7.1.

The light levels in the shed ranged from 1.5 to 24 Wm^{-2}, averaging around 7 Wm^{-2}; compared with outdoor levels averaging around 350 Wm^{-2}. That is, indoor levels were around 2% of outdoor levels. The air temperature in the shed ranged from 13 to 24 degrees, and was similar to that measured outside (refer Table 3.6).

1.2.2 Strobilus Production

These data are presented in Table 7.2.

The conditions in the seed extractory shed were adverse for seed-cone bud differentiation, and also for health of the grafts. Regardless of the date grafts were moved into the shed, those that were held in for either 42 or 56 days failed to differentiate seed-cone buds; and some became chlorotic and died. Only a few grafts that were held in for 28 days carried strobili. The results presented in Table 7.2 are only for grafts that were inside the extractory shed for 14 days.

The results in Table 7.2 indicate that when grafts were away from the seed orchard for the second half of February or the first half of March, they did not carry strobili at anthesis. There was an apparent period of time when grafts in the shed did not receive the environmental stimulus necessary for strobili to develop. This time period was apparently greater for clone 268-514 than for the other two clones.

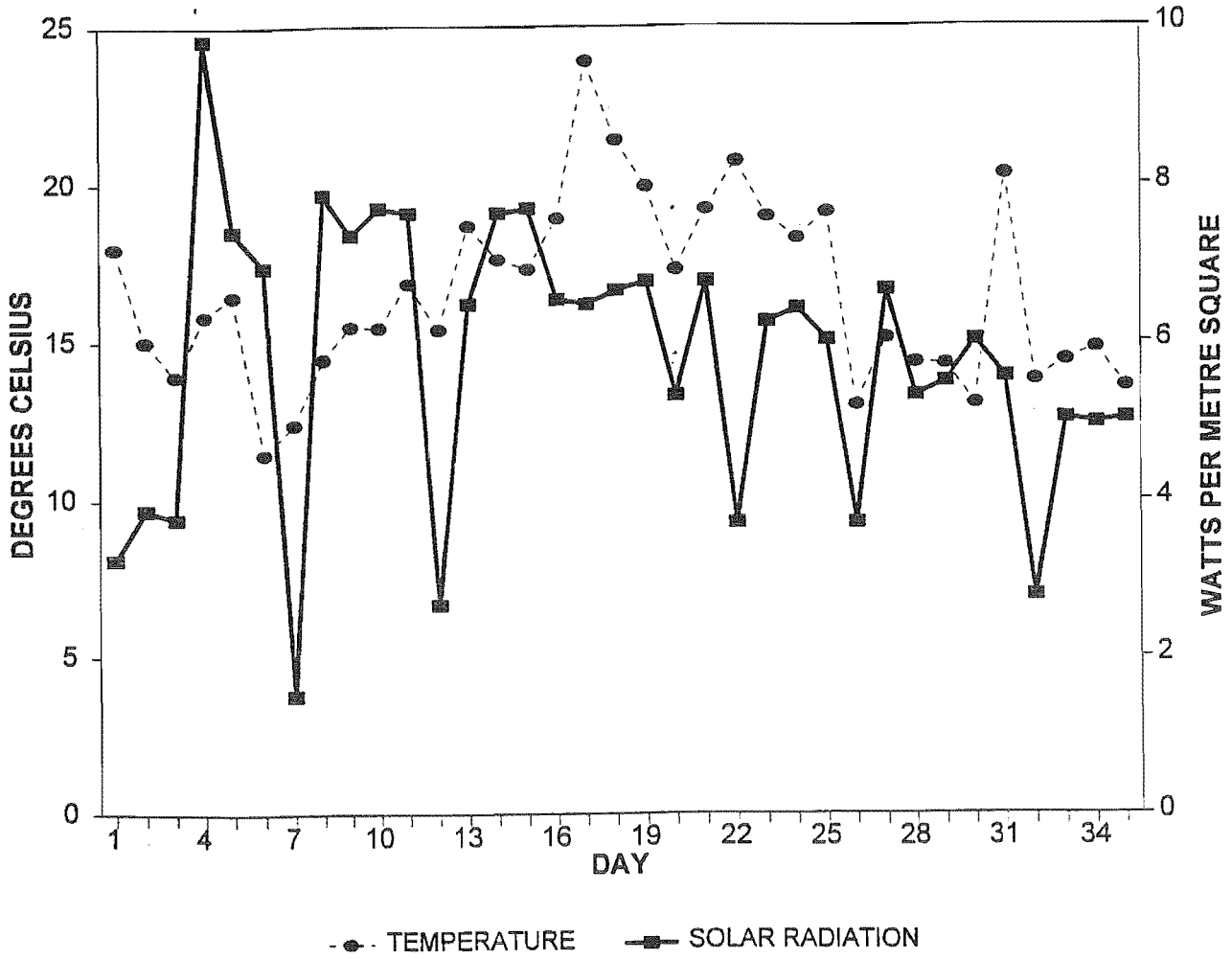

Figure 7.1

A graph of the temperature (°C) and solar radiation (Wm^{-2}) conditions inside the seed extraction shed over a 35 day period of the experiment. Measurements began on the 1st of February 1993 and finished on the 7th of May 1993. Data are presented for February 1993 and the beginning of March 1993.

Table 7.2

The effect of sequential transfers of potted grafts to a seed extractory shed during the summer months on percent of grafts that carried strobili, and the number of strobili per first annual cycle of growth. The latter data are presented as means per graft (±SE).

Transfer-period to shed	Clone 268-54		Clone 268-514		Clone 268-109	
	%	Number	%	Number	%	Number
1 Jan. - 15 Jan.	100	4.0 ± 1.1	66	3.5 ± 0.4	66	1.7 ± 0.7
15 Jan. - 29 Jan.	100	4.3 ± 1.2	66	3.0 ± 0.6	66	1.5 ± 0.4
29 Jan. - 12 Feb.	33	4.0 ± 0.0	0	0.0 ± 0.0	66	2.0 ± 0.8
12 Feb. - 26 Feb.	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
26 Feb. - 12 March	0	0.0 ± 0.0	0	0.0 ± 0.0	0	0.0 ± 0.0
12 March - 26 March	100	2.3 ± 0.9	33	3.0 ± 0.0	33	3.0 ± 0.0
Control	100	4.0±0.57	66	2.6 ±1.4	100	3.3 ± 0.8

1.3 DISCUSSION

There are 2 options for applying such treatments. It is possible to move plants from a non-strobilus producing to a strobilus forming environment for short periods of time, and hope to "capture" the strobilus differentiating stimulus. Or (as done in this experiment), plants can be moved out of a good strobilus producing environment for differential periods of time. It was felt that the approach chosen was more likely to yield "sharp" results, and this was borne out by the results.

As indicated in the Introduction to this chapter, treatments were applied at a time when it was expected that first cycle long shoots would have been initiated, but not fully differentiated. Hence the selection of January, February and March as the treatment months. Because it was not known how long a period away from the strobilus-forming stimuli would be necessary, duration of transfer (from 2 to 8 weeks) was tested along with time of transfer.

The results indicated that when the period of long-shoot bud development between mid-February and mid-March was not associated with normal light conditions, seed-cone buds were not differentiated. This result is consistent with information from the correlation analysis in Chapter 4, that numbers of emergent strobili at anthesis are correlated with a climatic event at that time.

It is of interest to compare the timing shown up in this experiment with that found by Siregar (1994) in his studies of $GA_{4/7}$ application. Working in the same year (1993) as Experiment 1 was carried out, in the same seed orchard, and using 2 clones in common, Siregar established that the optimum strobilus-forming response from $GA_{4/7}$ application to buds, was with applications between the 17th and the 25th of February. It fell off quite rapidly, however, after the 1st of March. Thus in terms of the query raised in the Introduction to this chapter, the evidence so far would support the view that environmental and chemical strobilus-forming stimuli are working on the same biological processes at the same time.

However, the evidence from Chapter 3 of the impact of weather subsequent to strobilus differentiation does need recalling, along with the literature reporting similar events (e.g., Silen, 1973a; Sweet, 1975). In that context, an experimental design which kept all material in a uniform environment after treatment was important.

While it is likely that the main environmental variable affecting strobilus differentiation inside the extractory shed was light intensity, it is important to emphasize, that Experiment 1 *per se* does not indicate a role for light intensity in strobilus initiation. The very low levels of light in the cone extraction shed were well below levels at which radiata pine could remain healthy for long periods. What the experiment hopefully does do is indicate the timing during which appropriate environmental conditions are needed. The literature certainly does indicate the importance of light intensity in affecting strobilus production, but thinning studies, the consideration of edge trees, and the position of female strobili in the crown are likely to represent effects over longer periods of time than the treatment in this experiment.

2. SHADING EXPERIMENT (Experiment 2)

2.1 RATIONALE

The 1993 transfer experiment was extreme in terms of the levels of light reduction used. It was also very effective in identifying the seasonal time at which the direction of differentiating buds can be influenced.

In 1994, it was decided to repeat the experiment using more biologically acceptable levels of light reduction. The intention was to confirm the timing, particularly with respect to the importance of January, and also establish the levels of light reduction necessary to prevent strobilus differentiation.

2.1.2 Material

As for the transfer experiment potted grafts of three clones, all regarded as "reasonable flowerers" (Sweet, 1979), were used in this experiment. The grafts in this experiment were in their second year after potting.

The experiment was conducted according to a 3×2×3 factorial design, where grafts were shaded at 3 levels (100%, 70% and 30% full sunlight) either for the months of February and March, or for a period from mid-January (17th January) to the end of March. These treatments were tested across the same 3 clones as in the transfer experiment. There were 6 replicate ramets in each of the 18 treatment groups, giving 108 ramets in all.

2.1.3 Shade Houses

Two shade houses were constructed, covered in shade cloth that blocked out either 70% or 30% of the light, respectively. Six grafts of each of 3 clones were moved into each shade house, either in the middle of January or at the beginning of February. All grafts were returned outside at the end of March. As for Experiment 1, the temperature and light conditions were recorded in each shade house during the experiment.

2.1.4 Gibberellin $A_{4/7}$ Application

On the 23rd of February 1994, all ramets received a dose of 25mg of crystalline $GA_{4/7}$ via a stem injection application. The gibberellins were dissolved in 95% ethanol, and a 0.5ml of this solution was injected into a 0.5mm hole drilled at the base of each ramet. Both the dose rate and method of application represent standard practice in New Zealand seed orchards for the treatment of 2-year-old grafts.

The same assessments, as for the transfer experiment, were made on grafts at anthesis.

2.1.5 Statistical Analysis

Statistical analysis was done using PROC GLM and Fisher's protected LSD test (SAS Institute, 1987). A factorial analysis of variance (ANOVA) was used to test all the main and interaction effects resulting from timing and shading treatments across clones. The F tests for all effects discussed are significant at the 5% level. On the basis of the Fisher's protected LSD test, significant differences are at the 5% level. Data are presented as means with conventional LSD symbols. Variance quoted in the text is ±SE.

2.2. RESULTS

The treatments for this experiment were designed to build on and refine the results of Experiment 1. Clearly, the light intensity in the extraction shed impacted on seed-cone differentiation, but this was inevitable as levels were adversely low for plant growth. Thus it was intended in this experiment to use more subtle light reductions during seed-cone bud differentiation and determine what effect these had on the numbers of emerging strobili.

The results for this experiment are presented in Figures 7.2 and 7.3.

The percentage reduction in solar radiation by the "30%" and the "70%" shade cloth treatments was not exact (see Figure 7.2). The actual % reduction depended somewhat on the brightness of the day. However, across the duration of the experiment, the average reductions for the 30% and 70% treatments, respectively, were 46.4±5.0% and 62.2±4.4%. In terms of temperature, Figure 7.3 indicates little impact of shading on temperature, although there was a problem with the temperature sensor in the control treatment (ambient) for January, and the data are not available.

Table 7.3 indicates considerable variability in strobilus number within treatments. Overall the shade treatments did not have any significant effect on strobilus number.

However, both shade treatments significantly reduced the number of branches and latent buds per whorl (Table 7.4). Compared to the control treatment, the 30% and 70% shade treatments reduced branch number, respectively, by 43.7% and 76.0%. Both those treatments reduced latent buds, respectively, by 50% and 42%.

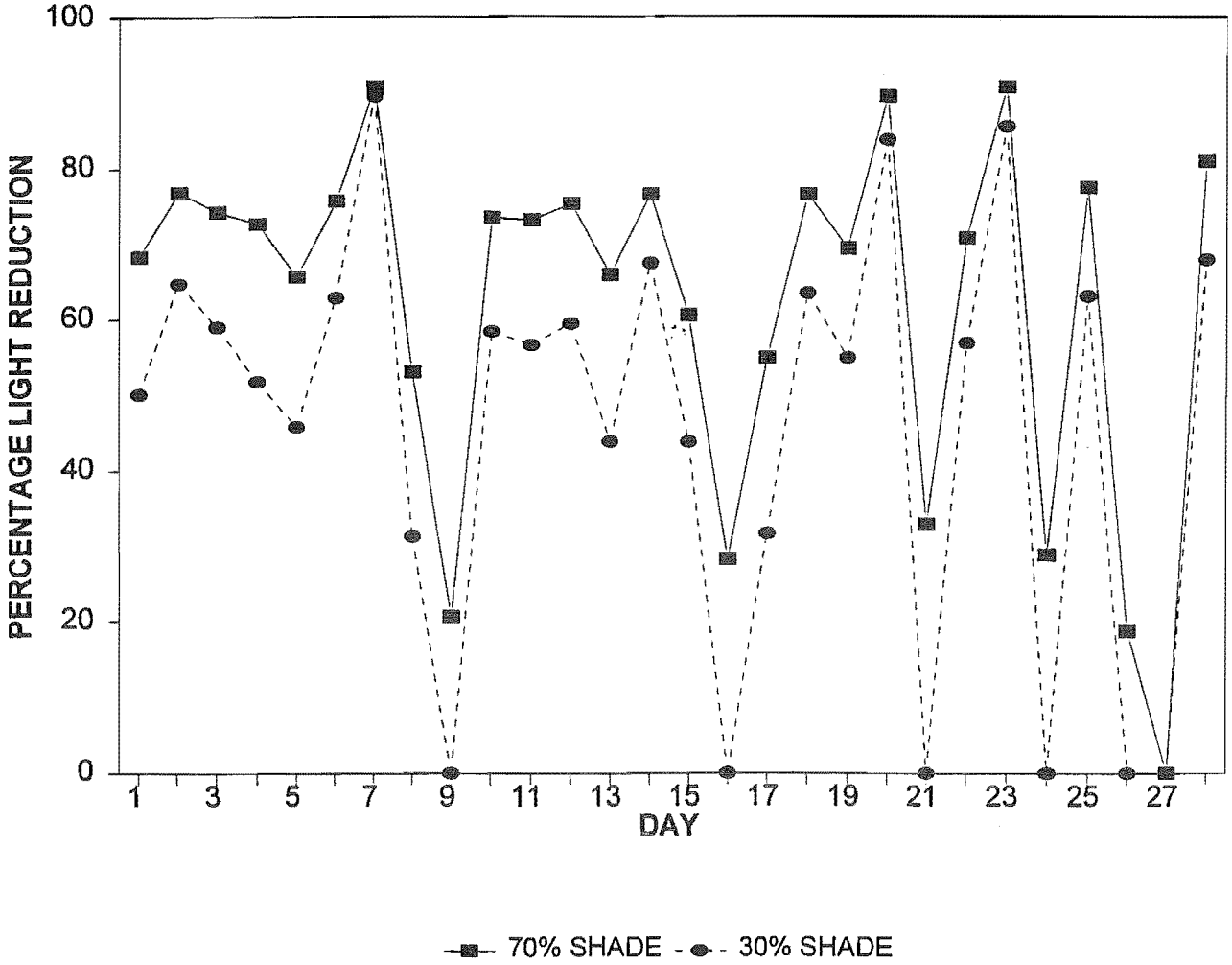

Figure 7.2

The percentage reductions (compared to ambient) in PAR in the 30% and 70% shade house treatments. Measurements were made during February 1994.

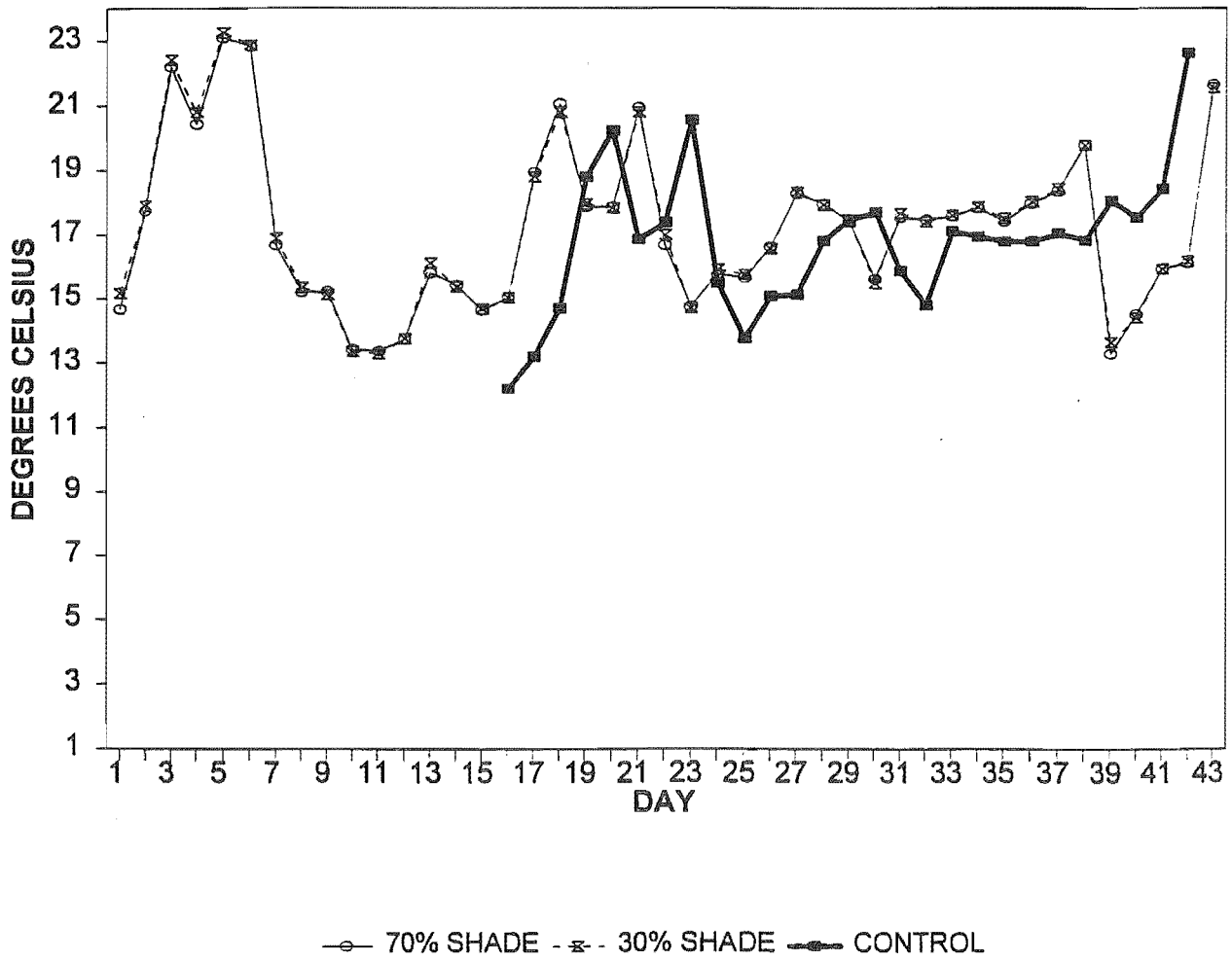

Figure 7.3

The temperature of ambient air compared to that inside the 30% and 70% shade house treatments. Measurements began on the 17th January 1994. Due to a technical problem with the temperature sensor, data were not recorded during January 1994.

Table 7.3

The effect of shading treatments on the number of emergent strobili per whorl. All treatments were across 3 clones and grafts were either shaded from the middle of January 1994 to the end of March 1994 or for the whole of February 1994 and March 1994. The data are presented as mean values per graft ± SE.

Clone	Month of commencement of shading	Shade (% full sun light)	Strobili
268-54	January	Control	2.7 ±0.9
		30	0.5 ±0.4
		70	2.2 ±1.4
	February	Control	1.6 ±1.0
		30	3.4 ±1.5
		70	0.0 ±0.0
268-109	January	Control	3.2 ±1.6
		30	4.3 ±1.1
		70	2.2 ±1.1
	February	Control	3.5 ±0.5
		30	2.0 ±0.8
		70	5.0 ±1.5
268-514	January	Control	4.0 ±1.0
		30	2.3 ±0.8
		70	3.3 ±1.4
	February	Control	2.5 ±1.5
		30	1.0 ±0.6
		70	0.8 ±0.7

Variable	[1] Significance (Pr> F)
Clone	0.0063
Shade	0.2483
Date	0.1150
Clone × Date	0.1396
Clone × Shade	0.8334
Clone × Shade × Date	0.0232

[1] Significance testing was carried out on $\log_e$-transformed data.

Table 7.4

The effect of shading treatments on the number of branches and latent buds per whorl. All treatments were across 3 clones and grafts were either shaded for the whole of February and March or from the middle of January to the end of March. The data are presented as mean values per graft.

Shade treatment	[1] Branches	[1] Latent buds
Control	0.96[a]	1.48[a]
30%	0.54[ab]	0.74[b]
70%	0.23[b]	0.86[b]
Variable	[2] Significance (Pr> F)	
Clone	0.1370	0.6075
Shade	0.0235	0.0230
Date	0.2525	0.3790
Clone × Date	0.0878	0.0647
Clone × Shade	0.7822	0.1003
Clone × Shade × Date	0.4149	0.2546

[1] Values without a common letter differ at the 5% level as per a Fisher's Protected LSD test.

[2] Significance testing was carried out on $\log_e$-transformed data.

2.3 DISCUSSION

The results of this experiment indicated that, unlike the severe light reduction treatment in the first experiment, more subtle shading treatments had little effect on the numbers of emergent strobili at anthesis. The experiment was thus unsuccessful in confirming the timing at which long-shoot differentiation can be influenced by treatment.

It appears that light reduction impacted more on vegetative growth than reproductive growth, and the timing was not significant in this respect. It was found that the shading treatments significantly reduced the number of branches per whorl, as well as latent buds. Thus it is likely that reduced light would impact on strobilus production in the longer term by restricting crown growth.

It is known that when crown development is restricted the number of sites for strobilus initiation is limited. In the long term decreased branch number would restrict crown growth and in turn the number of sites for strobilus initiation. Silen (1973b) reported shading to have a negative effect on strobilus production in *Pseudotsuga menziesii* trees, but only in the second year of treatments. Some ameliorative strobilus treatments, for example nitrogen fertiliser application, work in a reverse manner to shading effects by increasing branching and thus increasing the number of coning sites in the crown.

In summary, although in the short term it was not evident that shading in this experiment reduced strobilus number, its effect on branch number would implicate low light levels along with suppressed crown growth as reducing strobilus production in the longer term.

C. GENERAL DISCUSSION

The experiments reported in this chapter set out to gain further understanding on the time period when seed cone bud differentiation can be most influenced by environmental conditions.

In summary, the results reported in this chapter support the view of Bollmann (1983), that in *Pinus radiata* grafts, the period of time of seed cone-bud differentiation encompasses the last two weeks of February. This supports information from the strobilus production model (Chapter 4) that air temperature and soil water stress during February and March influence numbers of emergent strobili. And it is in turn supported by the $GA_{4/7}$ timing experiments of Siregar (1994).

At the time when the studies were being carried out, it was assumed that during the second half of February , long-shoot buds have been initiated; and the period of late February / early March probably encompasses the early stages of them becoming microscopically recognisable as branch buds or strobili. However, subsequent to that, research in Amberley seed orchard by Dickson, Riding and Sweet (1994) revealed that the initiation of long shoot primordia in recently planted meadow orchard ramets was very much later than occurred in the older grafts and forest trees which had been sampled prior to that (See Appendix A). Thus, although the second half of February was confirmed as a key time to influence strobilus numbers in young meadow orchard grafts, the stages of bud development then were not as expected.

Because the important component was the timing, rather than the stage of bud development, it was accepted that subsequent strobilus production treatments at Amberley seed orchard should be applied during the second half of February.

The results of the shading experiment indicated that reducing light levels by up to 60% during the period from mid-January to the end of March had no significant effect on the numbers of seed-cone buds that developed. However, the treatments did affect branch bud differentiation suggesting that limited light reduction affects strobilus production patterns only in the longer term, by restricting crown growth.

CHAPTER 8

THE EFFECT OF TEMPERATURE ON STROBILUS DIFFERENTIATION AND DEVELOPMENT

A. INTRODUCTION

The empirical strobilus model developed in Chapter 4 indicated that air temperature during February, and to a lesser extent during May, was correlated with mean numbers of emergent strobili counted in stands of *Pinus radiata*, across sites and climates. The independent variable mean daily minimum temperature of February was found to explain over 50% of between-site variability in numbers of emergent strobili.

The literature also implicates temperature with strobilus production in conifers, both at the forest stand level and in potted trees (see Chapter 2).

The majority of mast seeding studies have concluded that of all the climatic variables, air temperature during the time of bud initiation is the variable that is most often correlated with mast seeding (Van Vredenburch and La Bastide, 1969; Holmsgaard, 1972; Fober, 1976). Generally elevated temperatures favour seeding, but there are reports of species that will only mast when unusually cool temperatures prevail during bud initiation (Norton and Kelly, 1983).

Temperature clearly has a profound influence on reproductive processes in conifers (see Chapter 2). It has been shown experimentally that conifers produce more male and female strobili when temperatures are elevated during the time of bud differentiation (Chalupka and Giertych, 1977; Owens, Philipson and Harrison, 1982). The mechanism by which temperature affects the number of seed-cone buds differentiated is largely unclear (Ross, 1989). It has, however, been proposed that it is probably a physiological one, with temperature affecting growth rates within the long shoot region, and that in turn promoting the development of structures with reproductive potential. However, an alternative proposal that high temperature stress leads to the accumulation of non-polar gibberellins in the shoots, which in turn promotes reproductive activity, should not be discounted (Chalupka, Giertych and Kopcewicz, 1982;

Webber *et al.*, 1985).

Based on the findings of the survey reported in Chapter 4, supported by the literature reviewed above, experiments were designed to explore the impact of temperature on *Pinus radiata* strobilus production, during differentiation and subsequent development. Two experiments were planned, one to explore the significance of temperature during the general period of February and March, a treatment time which had been shown to be particularly effective (Chapter 7); and one during the months of May through to August which were implicated in Chapter 3 as being important.

B EXPERIMENTS

1. SUMMER AIR TEMPERATURE EXPERIMENT

1.1 MATERIALS AND METHODS

1.1.1 Site

This experiment investigated temperature effects during the period mid-January 1994 to end of March 1994 inclusive on strobilus production at Amberley seed orchard.

1.1.2 Material

In this experiment, potted grafts of the four orchard clones (268-54, 268-514, 268-109 and 850-55) in their second year following potting were used. They were propagated and grown as described in Chapter 7.

1.1.3 Experimental Design

This experiment was conducted according to a 5×4 factorial design, including 5 temperature treatments applied across 4 clones. There were 6 replicate grafts in each of the 20 treatment groups, giving 120 ramets in the complete experiment.

The temperature treatments were started on the 15th of January 1994 and stopped at the end of March 1994.

1.1.4 Gibberellin $A_{4/7}$ Application

On the 23rd of February 1994, all ramets received a dose of 25mg of crystalline $GA_{4/7}$ via a stem injection application. The gibberellins were dissolved in 95% ethanol, and a 0.5ml of this solution was injected into a 0.5mm hole drilled at the base of each ramet.

1.1.5 Treatments

The 5 individual treatments were as follows:

(i) Cooling Treatment

Grafts were cooled by a mist generated by misting nozzles (see Plates 8.1 and 8.2). An automatic timer was constructed and connected into the hose line supplying water to the nozzles. This timer switched the nozzles on for one minute in every five. That time interval was long enough for the crowns of the grafts to be wetted to run off. Following the switching off of the nozzles the moisture evaporated from the crown causing a cooling effect (latent heat of evaporation). Heat was lost from the shoots by convection. A thermostat controlled the overall system; and was set at 15°C. Thus, the nozzles did not operate when the ambient temperature was below that threshold.

To ensure the cooling effect was not confounded by a modified plant water potential caused by run-off from the misting, each pot was enclosed in a plastic bag, sealed at the top around the stem of the graft.

The soil water potential chosen for the experiment was -1.5 MPa (Volumetric water content = 0.65 cm^3cm^{-3} - wilting point). This was based on daily estimates of the soil water balance model for February 1993 reported in Chapter 9. It was considered appropriate that grafts should be growing in water stressed soil in this temperature experiment, as the field-sites in Chapter 4 that had warm summer temperatures were also generally dry. To maintain the required soil water levels, water was injected through the wall of the plastic bags onto the growing media.

(ii) Polyethylene House

A polyethylene house was constructed to warm grafts (Plate 8.3). The polyethylene covering that was used was called "Agphane" and was obtained from Harford Greenhouses Ltd, Christchurch, New Zealand. In an attempt to prevent the inside air temperature rising too high a ventilation system was installed. This comprised an extractor fan that drew warm air from inside and replaced it with fresh air drawn in through a duct located in the roof of the house. The extractor

fan was controlled by a thermostat that switched it on when the ambient temperature rose above 15°C.

To further control temperature a commercially produced liquid sun-filter (produced by "Kiwicare") which was sprayed onto the inside and outside of the covering of the house to assist with the prevention of excessive heat build up. Open trays of water were placed around on the floor to help maintain the relative humidity of the air at around 60%.

As for the grafts in the cooling treatment, water potential of the growing media was maintained at -1.5 MPa.

(iii) Pollination Bags

In 2 treatments, pollination bags were used to increase the temperature around shoots with strobilus-bearing potential. Individual shoots on grafts were enclosed in either a cellulose or polyester pollination bag - the same bags that are used for controlled pollination crosses (see Plate 8.4).

The different pollination bags were selected with the intention of differentially heating graft shoots. It was thought the polyester product would reflect heat away to some extent and thus not warm the shoot as much as the clear cellulose material.

Again, the water potential of the growing medium in each pot was maintained at -1.5 MPa.

(iv) Control Treatment

The control grafts were sited next to those treated with pollination bags, and close to those in the polyethylene house and cooling treatments. Their growing medium in each pot was maintained at -1.5 MPa.

1.1.9 Environmental Measurements

Maximum, minimum and mean temperatures were measured in the polyethylene house the pollination bags and outside, using a thermistor temperature sensor. The levels of photosynthetically active radiation (PAR) in the polyethylene house and outside were measured with Licor quantum sensors.

Campbell CR10 data loggers were used to record, on a daily basis, air temperature, soil temperature and light conditions over a 24hr period. The loggers were programmed to take an iterative sample every 6 minutes, and then over a 24hr period calculate a maximum, mean and minimum value for temperature, and a total value for light (PAR). The logger in the polyethylene house began recording on the 17th of January 1994, while the one outside started on the 1st of February 1994. Both loggers recorded up until the end of March 1994.

Monitoring capability was at all times restricted by the amount of available equipment. One impact of this was that temperature was only able to be recorded in the polyester bags for the first half of February and in cellulose bags for the second half of February. Further, the data logger used to record temperature in the pollination bags malfunctioned. As a result it has not been possible to compare temperatures in the pollination bags with the ambient control temperature.

Additionally, limited bud temperature monitoring was also carried out. For 17 days in the first half of March, miniature thermocouples connected to Campbell CR10 dataloggers were used to measure the temperature of terminal buds on grafts in the polyethylene house, under the misting nozzles and under ambient conditions. The thermocouples were made up using Copper-Constantan wire. The diameter of each thermocouple wire was 0.5mm, and for each treatment a thermocouple wire was inserted into a representative terminal bud.

Although the bud temperature measurements were made in March 1994 they were considered to be indicative of the relative temperature differentials between treatments during part of January 1994 and for the whole of February 1994.

1.1.10 Assessments

At the end of August 1994 the numbers of emergent strobili, branches and latent buds in the first annual cycle of grafts were counted. Because ramet size was relatively small, only the first annual cycle of growth carried strobili.

1.1.11 Statistical Analysis

Statistical analysis was done using PROC GLM and Fisher's protected LSD test (SAS Institute, 1987). A factorial analysis of variance (ANOVA) was used to test all the main and interaction effects as a result of temperature treatments across clones. The F tests for all effects discussed are significant at the 5% level. On the basis of the Fisher's protected LSD test, significant differences are at the 5% level. Data are presented as means with conventional LSD symbols. Variance quoted in the text is ±SE.

Plate 8.1

A general view of the wooden frame from which the misting nozzles and their associated piping was hung. In this photograph the system is switched on. Graft planter bags are shown enclosed in plastic.

Plate 8.2

A close up view of the misting nozzles showing the fine mist of water they produced.

Plate 8.3

A photograph of the polyethylene house used to warm grafts from the 17th of January 1994 through to the 31st of March 1994. The extractor fan installed to circulate air for temperature regulation is shown.

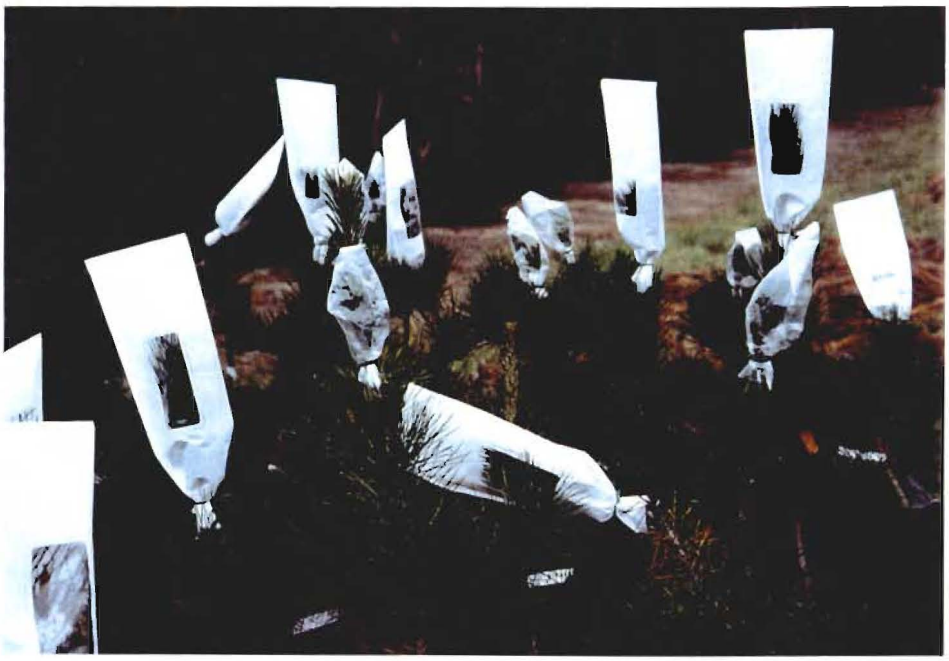

Plate 8.4

A photograph of the cellulose and polyester pollination bags used to warm graft shoots from the 17th of January 1994 through to the 31st of March 1994. The polyester bags appear white whilst the cellulose bags are transparent.

1.2 RESULTS

1.2.1 Air Temperature

(i) Ambient Air

The mean temperature of ambient air measured for a 59 day period starting on the 1st of February 1994 was 15.1°C (Table 8.1). The maximum and minimum were 21.0°C and 9.4°C respectively.

(ii) Polyethylene House

These results are presented in Table 8.1.

The air temperature in the polyethylene varied from day to day. Over the 73 day period beginning on the 17th of January 1994 the average maximum air temperature in this treatment was around 30.4°C, and on 5 days during this period it rose over 39.0°C; on one day it reached 40.0°C. The mean temperature was 20.0 °C. The mean maximum temperature inside the polyethylene house was 45% greater than ambient, while the mean minimum temperature was 37% greater.

(iii) Pollination Bags

Because of a datalogger malfunction, no temperature data can be presented for the pollination bags.

1.2.2 Bud Temperature

These data are presented in Table 8.2.

It should be recalled that the bud temperature measurements were made only during the first 17 days of March 1994. Nonetheless, the relativity of these measurements between treatments are regarded as indicative of patterns of bud temperatures for the whole period mid-January 1994 to the 31st of March 1994.

The mean temperature (thermocouple) of buds in the polyethylene house and under the cooling treatment was 18.5°C and 12.4°C, respectively. The mean temperature of buds in the ambient air treatment (outside) was 14.1°C.

The mean maximum temperature reached by buds in the polyethylene house was 62.6% higher than that of ambient air buds which in turn were 10.2% higher than that of buds in the cooling treatment.

1.2.3 Solar Radiation

Refer to Figure 8.1.

The level of photosynthetically active radiation (PAR) in the polyethylene house was more uniform than that outside. Averaged over the period as a whole, the PAR inside the polyethylene house was only 65% of that outside.

1.2.4 Numbers of Emergent Strobili, and Long Shoot Differentiation

These results are presented in Table 8.3.

The temperature treatments had a significant effect on strobilus production in the first annual cycle of growth with the clone×treatment interaction being non-significant. The most striking effect was the total lack of strobili in the polyethylene house treatment. Compared to the control treatment, the cooled treatment reduced the number of strobili produced by 44.3%, whilst the cellulose bag and polyester bag treatment (data not presented) had no significant effect on strobilus production.

The treatments also affected the total number of long shoot components, and their composition. In the polyethylene house there were significantly fewer total long shoots than in the ambient control, and those that were present were essentially branches. There were virtually no latent buds, and of course no strobili. Compared with the control, the cooling treatment significantly affected only strobilus number, and no other long shoot components.

Values for the pollination bag treatments are not presented in Table 8.3 (or Table 8.4) because the of the lack of temperature data precludes their sensible interpretation. Overall, however, the use of pollination bags had little effect on the number of strobili carried by trees.

1.2.5 Percent of Grafts that Produced Strobili

These results are presented in Table 8.4.

The percentage of control grafts bearing strobili was variable across clones. No grafts in any clones formed strobili in the polyethylene house treatment.

The cooling of buds resulted in fewer grafts producing strobili, across all clones. In clone 268-109, 80% fewer grafts produced strobili in the cooling treatment compared to the control treatment. Across all clones the drop was 43.6%.

Table 8.1

Air temperature measurements inside the polyethylene house treatment and for ambient air. The data inside the polyethylene house were recorded for a 73 day period beginning on the 17th of January 1994. Ambient air temperature measurements were made for a 59 day period beginning on the 1st of February 1994. Data are presented as mean values ±SE.

Treatment	Temperature	°C
Polyethylene house	Maximum	30.42±3.86
	Mean	20.07±0.39
	Minimum	12.95±0.36
Ambient air	Maximum	20.98±0.66
	Mean	15.09±0.48
	Minimum	9.46±0.49

Table 8.2

Terminal bud temperature measurements of grafts in the polyethylene house, in the cooling treatment and in ambient air. Measurements were made from the 1st-18th of March 1994 with a thermocouple wire inserted into one bud in each treatment. Data are presented as mean values ± SE.

Treatment	Temperature	°C
Polyethylene house	Maximum	38.70±1.59
	Mean	18.50±0.55
	Minimum	9.25±0.79
Ambient air	Maximum	23.80±0.91
	Mean	14.11±0.65
	Minimum	8.77±0.81
Cooling treatment	Maximum	21.60±1.11
	Mean	12.42±0.49
	Minimum	7.66±0.83

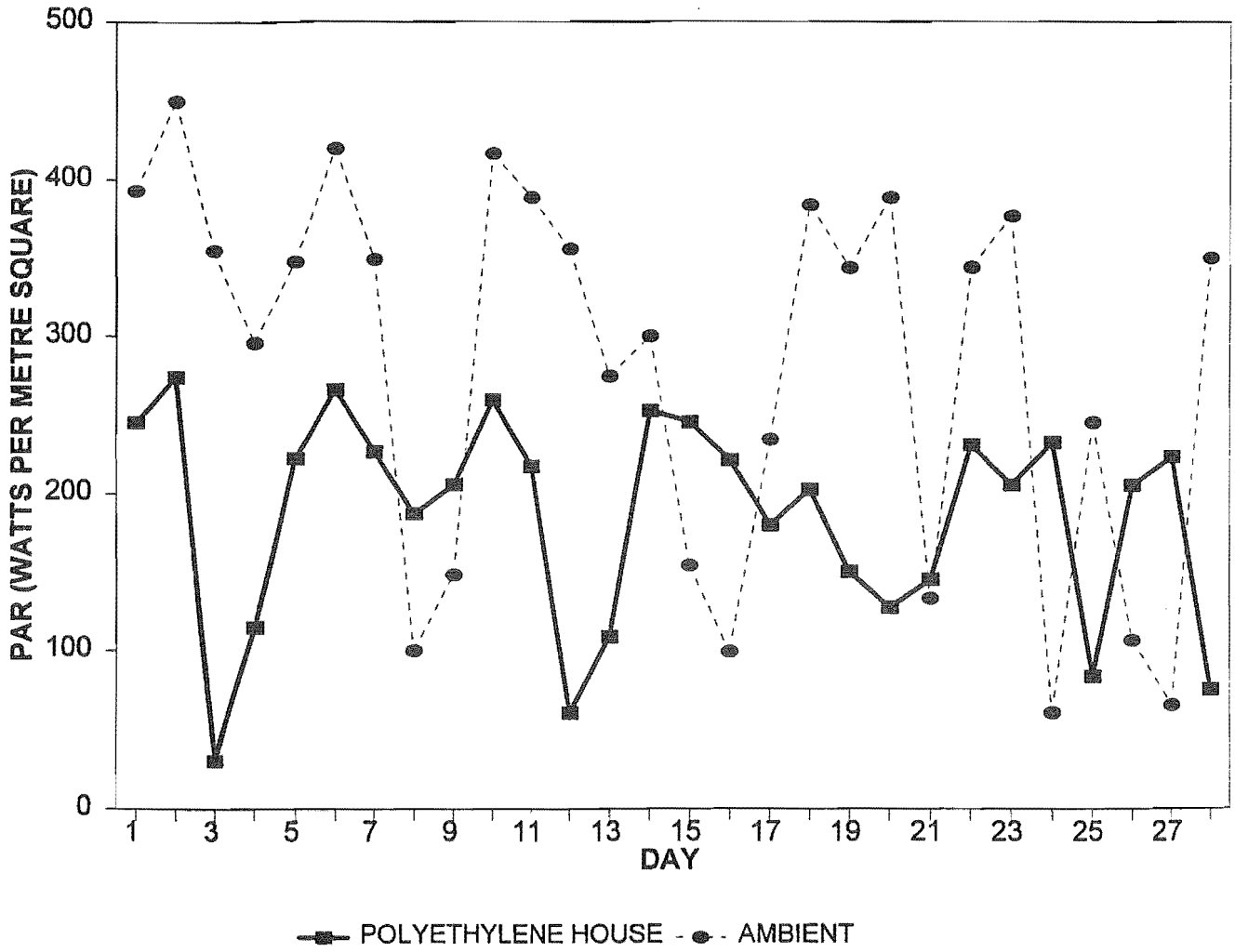

Figure 8.1

A plot of the mean levels of photosynthetically active radiation (PAR) inside the polyethylene house and under ambient conditions

Table 8.3

The effect of temperature treatments on the number of emergent strobili, branches, latent buds and total long shoot components in the first cycle of annual growth. The temperature treatments began on the 17th of January 1994 and finished on the 31st of March 1994. The data are presented as mean values per graft.

Temperature treatment	[1] Strobili	[1] Branches	[1] Latent buds	[1] Total long shoot components
Ambient	2.21[a]	1.00[a]	1.65[a]	4.86[a]
Cooling treatment	1.23[b]	0.72[a]	2.23[a]	4.18[a]
Polyethylene house	0.00[c]	0.61[a]	0.05[b]	0.66[b]
Main effects	[2]Calculated probability level (Pr>F)			
Clone	0.1941	0.0119	0.4192	0.7714
Treatment	0.0001	0.0029	0.0001	0.0001
Clone×Treatment	0.0859	0.0177	0.4831	0.1288

[1] Values without a common letter differ significantly at 5% by Fisher's Protected LSD test.

[2] Significance testing was carried out on $\log_e$-transformed data.

Table 8.4

The effect of temperature on the percentage of potted grafts that carried strobili in four orchard clones. The temperature treatments began on the 17th of January 1994 and finished on the 31st of March 1994. The data are presented as mean values per treatment.

Temperature treatment	Clone			
	268-54	268-514	268-109	850-55
	% of grafts that produced strobili			
Ambient	71	57	100	75
Cool	23	36	20	50
Polyethylene house	0	0	0	0

1.3 DISCUSSION

The intent of this experiment was to establish in clonal grafts whether temperature during the summer impacts on the number of strobili carried by grafts at anthesis.

Across all clones, cooling buds during part of January and all of February and March significantly reduced strobilus production. So also did the warming treatments: none of the grafts held in the polyethylene house produced strobili.

In this experiment the polyethylene house treatment reduced total long shoot bud component number production and eliminated female strobilus production. This was a surprising result considering the overwhelming evidence in the literature that in conifers elevated temperatures strongly promote female and male strobilus production. Tompsett and Fletcher (1979) reported increasing strobilus production in Norway spruce by moving potted trees into a polyhouse. Working with field-grown *Pinus sylvestris*, Chalupka (1981) reported significantly increasing female and male strobilus production on lateral shoots that had been enclosed in polyethylene bags for 6 weeks during the mid-summer. It also appears that strobilus production in potted trees is more responsive to temperature elevation than crowns of field-grown trees (Chalupka and Giertych, 1977; Ross, Eastham and Bower, 1986).

Working with Norway spruce, Ross (1989) indicated that the movement of potted trees into a polyhouse heated to provide 30°C days and 20°C nights resulted in profuse female and male strobilus production. However it was pointed out in this reference that temperatures much above 30°C appeared to be deleterious for strobilus production.

From the air temperature data in this chapter, it is evident that the air temperature in the polyethylene house reached above 35°C. Indeed on one day in February the air temperature rose above 40°C. Although considerable effort went into developing systems for cooling the polyethylene house air temperatures probably still rose too high for long shoots including strobili to develop. In fact the grafts showed symptoms of heat stress, namely the loss of apical dominance (Grace, 1983) along with some needle cast.

As well as increasing temperature the covering on the polyethylene house also reduced the PAR to 65% of ambient. It is unlikely, however, considering the results in Chapter 7 that this

effect would have reduced strobilus production in the short term. In Chapter 7, when the PAR levels were reduced to 70% of ambient, strobilus production was unaffected; although branch production, which may impact on strobilus production in the longer term, was reduced.

In the polyethylene house treatment the whole plant (roots and shoots) was warmed. There is a reference in the literature implicating strobilus production with suppression of signals coming from the roots due to temperature elevation (Philipson, 1983). However, this proposal has since been largely discounted by Ross (1989). Thus, heating of the roots in the polyethylene house treatment would not have been expected to significantly modify strobilus production levels.

Cooling had a pronounced effect on bud differentiation. It reduced total long shoot production and of those which were produced, a high number became latent. It is suspected that the conditions in the cooling treatment were such that a greater proportion of long shoot primordia failed to develop into either seed cones or branches, but remained as small latent buds.

In summary, the indication from the model developed in Chapter 4 that warm temperatures during February promote strobilus production has only partly been borne out by this experiment. Certainly reducing the temperature was highly effective at reducing strobilus numbers, but the experiment was not able to demonstrate increased strobilus numbers at higher temperatures.

A likely interpretation of this failure is that the temperatures reached in the polyethylene house were at times at a level which was too high for long shoot development. There is considerable support for this suggestion from the well-documented evidence (Lanner, 1966) that terminal hypertrophy in pines (where no long shoot development at all may occur on the leading shoot for several years) is much more prevalent in tropical than in warm temperate regions; and has never been reported from cold areas. Lanner (1966) reported trees where no long shoot production occurred for 6 years. Terminal hypertrophy is not uncommon in radiata pine in the northern parts of its range in New Zealand.

The long term mean maximum February temperature for the meteorological station with the warmest mean February temperature in New Zealand is 23.8°C (NZ Meteorological Service, 1983). The fact that temperatures in the polyethylene house frequently exceeded 35°C and on

one occasion exceeded 40°C indicates that grafts were put in an environment considerably hotter than they would normally meet in New Zealand.

There is little published information on the reproductive behaviour of radiata pine in areas which are warmer than New Zealand. The most tropical area from which it has been reported is the Island of Hawaii at a latitude of between 19 and 20 degrees North and an altitude of 1550m. Lanner 1966 reported radiata pine profusely producing strobili for 9 months of the year in an area called Kulani camp (at 1550m) where the mean monthly temperature for August (the Northern hemisphere equivalent of February) was14.3°C (see Appendix F). The corresponding mean maximum temperature for August was 20.9°C.

It would seem that temperatures of 35°C to 40°C may be outside the range within which radiata pine can develop long shoots in general and strobili in particular. It is unfortunate that the cooling system in the polyethylene house was not able to keep temperatures below 30°C.

Thus on balance, the experiment supports the findings of the model reported in Chapter 4, as far as it goes. There is still a clear need, however, to demonstrate that strobilus production can be increased by increasing ambient temperatures during February to a sensible level.

2. WINTER TEMPERATURE EXPERIMENT

2.1 MATERIALS AND METHODS

2.1.1 Sites

This experiment was conducted from May 1994 through to August 1994 inclusive across a range of sites on the Canterbury plain, including Amberley seed orchard. The sites chosen are listed in Table 8.5 and mapped in Figure 8.2.

Table 8.5

Site location and altitude

Site	Latitude	Longitude	Altitude (m)
Amberley beach	43°10'S	172°21'E	3.0
Amberley seed orchard	43°10'S	172°20'E	28.0
Darfield	43°29'S	172°08'E	190.0
Snowdon	43°22'S	171°32'E	364.0

Grafts were also placed in a glasshouse heated to around 20°C, at the University of Canterbury, Christchurch.

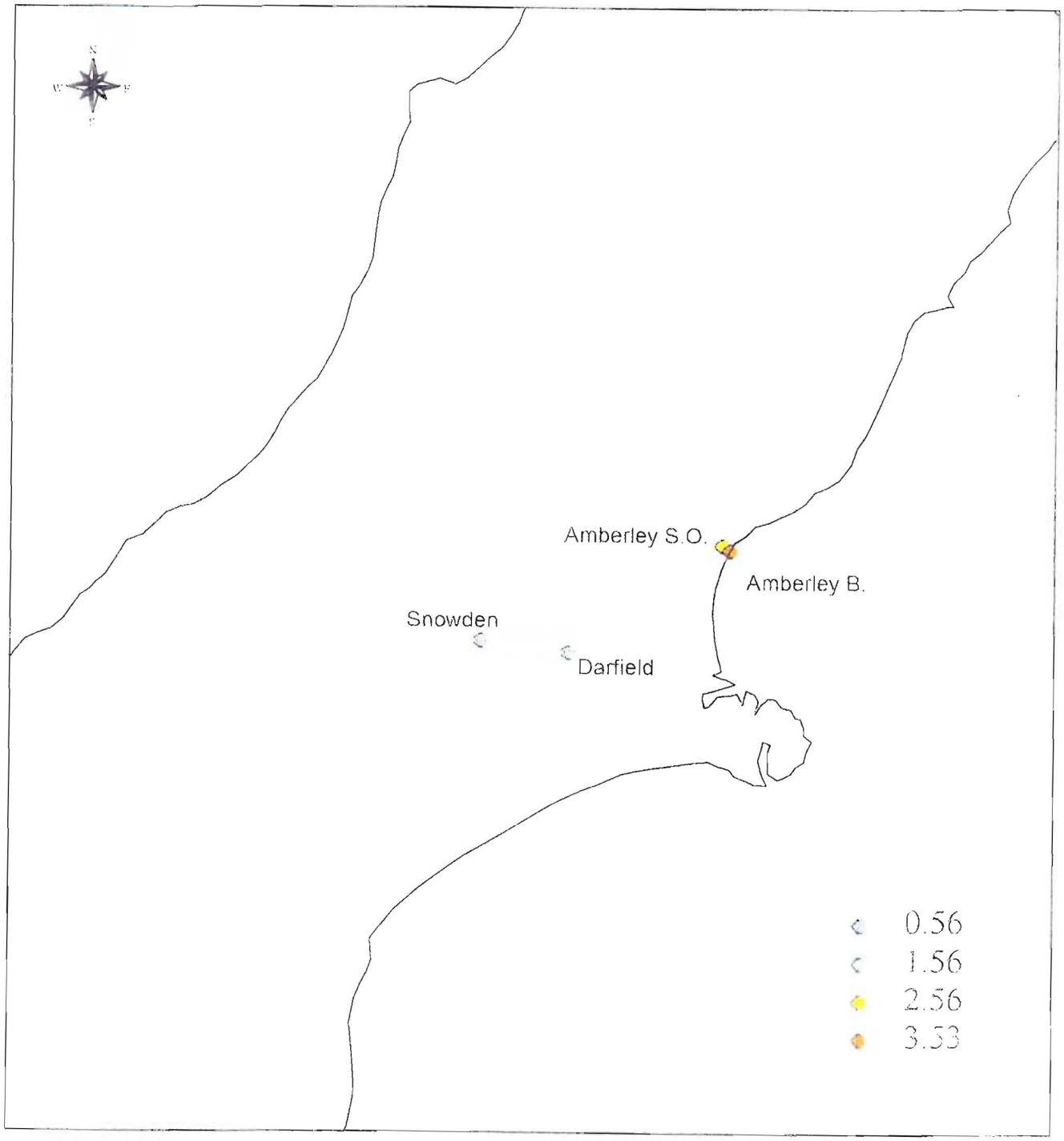

Figure 8.2

A map of the South Island illustrating the location of sites on the Canterbury plain at which grafts were located from May 1994 through to August 1994 inclusive. The average minimum temperature (°C) at each site for the months May through to August is depicted by a colour: which has a corresponding value.

2.1.2 Material

In late April 1994, after seed-cone bud differentiation had occurred, 120 representative grafts of clone 268-109 were selected, and divided into 6 groups of 20. All grafts were in their second year following potting. They had been potted, propagated and grown as described in Chapter 7.

2.1.3 Gibberellin $A_{4/7}$ Application

On the 23rd of February 1994, all ramets had received a dose of 25mg of crystalline $GA_{4/7}$ via a stem injection application. The gibberellins were dissolved in 95% ethanol, and a 0.5ml of this solution was injected into a 0.5mm hole drilled at the base of each ramet.

2.1.4 Terminal Bud Status

Following selection, terminal buds were harvested from 1 of the 6 groups of plants, and placed for 24hrs in FAA before being preserved in 70% ethanol. They were subsequently dissected and counts made of reproductive and vegetative primordia under a binocular microscope.

2.1.5 Graft Transfers

Four of the remaining 5 groups were then moved from the Amberley seed orchard to outdoor sites in Canterbury with different climatic conditions. The location of each site is given in Figure 8.2. The 5th set was moved to a glasshouse at Canterbury University, heated to around 20°C.

2.1.6 Experimental Design

The experiment was a completely randomised design comprising 5 treatments with 20 replicate grafts in each treatment.

2.1.7 Environmental Measurements

At each site, temperature was recorded on a daily basis. Iterative readings were taken every 6 minutes by CR10 dataloggers and were used to calculate mean, maximum and minimum value for each day. All sites except the one at Amberley beach and the glasshouse had automatic weather stations. At those sites temporary automatic weather stations were erected, as described in Chapter 3.

At the beginning of August 1994, all ramets were returned to Amberley seed orchard.

2.1.8 Assessments

At the end of August 1994 the numbers of emergent strobili, branches and latent buds in the first annual cycle of growth were counted. Because ramet size was relatively small, only the first annual cycle of growth carried strobili.

2.1.9 Statistical Analysis

Statistical analysis was done using PROC GLM and Fisher's protected LSD test (SAS Institute, 1987). A factorial analysis of variance (ANOVA) was used to test all the main and interaction effects as a result of site transfer treatments across clones. The F tests for all effects discussed are significant at the 5% level. On the basis of the Fisher's protected LSD test, significant differences are at the 5% level. Data are presented as means with conventional LSD symbols. Variance quoted in the text is ±SE.

2.3 RESULTS

2.3.1 Long Shoot Primordia Composition

The average number of seed-cone buds and other axillary primordia (branch + latent-buds) dissected from terminal buds harvested in April 1994 was, respectively, 4.35±0.41 and 4.29±0.32. The mean total number of long shoot primordia was 8.64±0.64.

2.3.2 Environmental Data

These data are presented in Table 8.6.

The air temperature at the coastal sites (Amberley beach and Amberley seed orchard) during the winter season was warmer than that at the inland sites of the Canterbury plain (Darfield and Snowden). As the winter progressed the temperature at all sites became cooler. At Snowden it was frequently below zero.

During the winter the total incoming solar radiation progressively declined at sites where it was recorded.

In the glasshouse the air temperature was warmer throughout the period measured than outside, and did not decline appreciably over the winter. The light levels, however, were significantly less than outside.

2.3.3 Numbers of Emergent Strobili

These data are presented in Table 8.7.

The number of emergent strobili counted on grafts kept at Amberley seed orchard, Amberley beach and Darfield was similar and did not differ significantly from one-another. However, the grafts at Snowden produced significantly fewer strobili than grafts at the other sites, and no grafts which over-wintered in the glasshouse produced strobili.

2.3.4 Loss of Strobili and Long Shoot Bud Components

These data are presented in Table 8.7.

At anthesis, grafts across all sites had lost around 13% of their total long shoot bud components; i.e., fewer long shoot bud components were present than were counted as axillary primordia prior to the winter. The mean total number of long shoot bud components counted across treatments was 7.48±0.29, compared with 8.64±0.64 in April. The grafts at the cool Snowden site lost a significant number of total shoot bud components.

The grafts held at the cooler Snowdon site and in the glasshouse carried significantly more latent buds than those at the Amberley sites. The glasshouse and Darfield grafts produced the most branches.

The glasshouse grafts produced greatly more (7.93±0.50) non-reproductive bud components than which were present as "other axillary primordia" the previous April (4.29±0.50). The grafts held at Darfield, Snowden, Amberley seed orchard and Amberley beach produced a decreasing number of non-reproductive buds, 5.20±0.30, 4.73±0.40, 4.37±0.35 and 4.09±0.51, in that order.

Table 8.6

Temperature and solar radiation data collected at sites at which grafts were held during the months May 1994 through to the beginning of August 1994 inclusive.

Site	Month (1994)	Temperature			Total Solar radiation (MJ m^{-2} d^{-1})
		max.	min. (°C)	mean	
Amberley beach	May	14.0	5.2	9.4	8.2
	June	11.0	2.3	6.4	5.4
	July	11.8	3.1	7.3	6.4
Amberley seed orchard	May	15.2	4.6	12.5	6.8
	June	10.5	1.4	5.9	4.5
	July	11.2	1.7	6.5	4.9
Darfield	May	13.3	3.7	8.5	[1]n/a
	June	12.1	0.3	6.2	n/a
	July	9.8	0.7	5.2	n/a
Snowden	May	11.5	2.9	7.2	n/a
	June	7.4	-0.8	3.3	n/a
	July	7.2	-0.4	3.4	n/a
Glasshouse	May	23.8	21.2	22.4	2.2
	June	20.6	15.8	18.4	1.2
	July	22.8	20.9	22.7	1.3

[1] Data not available

Table 8.7

The number of seed-cone buds and other axillary primordia counted in April 1994, and the number of emergent strobili, branches and latent buds per first annual cycle of growth in grafts held across a range of site winter climates. The data are presented as mean values per graft.

Treatment	[1] Strobili	Total long shoot bud components	Branches	Latent buds
April-harvested buds	4.35^{a}	8.64^{c}	4.29	
Glass house	0.00^{c}	7.93^{bc}	4.05^{c}	3.88^{b}
Amberley beach	3.21^{a}	7.30^{abc}	2.15^{ab}	1.94^{a}
Amberley seed orchard	3.23^{a}	7.60^{abc}	2.61^{abc}	1.76^{a}
Darfield	2.90^{a}	8.10^{c}	2.90^{bc}	2.30^{ab}
Snowdon	1.68^{b}	6.41^{a}	1.58^{a}	3.15^{b}
[2] Pr >F	0.0001	0.0408	0.0006	0.0358

[1] Values without a common letter differ significantly at 5% by Fisher's Protected LSD test.

[2] Significance testing was carried out on $\log_e$-transformed data.

2.3 DISCUSSION

Based on the results of this experiment, it is clear that the numbers of strobili and other types of long shoot are not "fixed" in the early pattern of differentiation. Site and climate during the months of May to July inclusive substantially modified the April pattern of differentiation. Differentiated strobili modified their direction of development to either become branches, or to remain latent.

Across all sites there was a loss of more than 10% of long shoot buds over the winter. This loss was a selective one. On the cold Snowden site significantly more seed-cone buds were lost than on the warmer Amberley sites. Further, at the cooler sites more differentiating buds ended up as latent buds. The glasshouse grafts also formed significantly more latent buds than those at the Amberley sites. It may be that increased latent bud production within whorls is associated with site environmental conditions not conducive to strobilus production, for example, inappropriate temperature regimes. Certainly in the previous experiment when grafts were artificially cooled in the summer, they tended to carry more latent buds within whorls.

Considering the effect of winter cold it might have been expected that the consistently warm temperatures in the heated glasshouse would ensure optimal seed-cone bud survival. This was, however, found not to be the case. That treatment caused the greatest loss of strobili of all, with all the differentiating buds switching to either branches or latent buds. It would appear that seed-cone bud differentiation requires an element of diurnal and probably seasonal variation to "lock" them in a reproductive pathway.

The plants moved to the glasshouse did not receive the normal pattern of seasonal cooling. By moving them into a heated glasshouse in May they went from a declining mean ambient temperature at Amberley seed orchard of 13.5°C (March, 1994) plus 12.4°C (April, 1994) to a glasshouse temperature between 15°C and 20°C.

Nor did they receive the diurnal temperature range they would have received outside. During the 3-month period in the glasshouse, the total temperature range was 8°C (from 15.8°C to 23.8°C). The typical diurnal temperature range was much less than that. This total is some 2°C less than that occurring naturally in the mildest parts of New Zealand over those months (N.Z. Meteorological Service, 1983).

Thus it seems likely that the interruption to the seasonal winter cooling, and/or the considerable reduction in diurnal temperature resulted in differentiated seed-cone buds "switching" to branch buds or becoming latent in their development.

The findings of this experiment support the literature (Silen, 1973a) and the data in the model (Chapter 4) in establishing that climatic conditions following the beginning of seed-cone bud differentiation (i.e., during May, June and July) can significantly affect the number of strobili reaching anthesis.

Unfortunately, due to the lack of potted grafts only one clone was available to establish whether winter temperatures played a role in strobilus development. Thus although the findings indicated that mild winter temperatures along with some seasonal cooling during the autumn were advantageous for strobilus production, these criteria may possibly not apply across all clones. Ideally, this experiment should be repeated across a range of clones.

C. GENERAL DISCUSSION

The intent of the experiments reported in this chapter was to verify the findings of the model in Chapter 4, that temperature during the time of seed-cone bud differentiation in February effects the number of emergent strobili at anthesis. Further, that temperature during May, some months after the beginning of bud differentiation, can modify the number of developing structures with reproductive potential. The treatments were not designed primarily to gain further understanding of the mechanisms of air temperature and strobilus production *per se.*

In both experiments cool treatments in January, February and March; and in May, June and July reduced strobilus production. These findings are consistent with those of the model (Chapter 4), in which both February and May temperatures were correlated with strobilus numbers across sites.

In neither experiment was it possible to successfully increase strobilus production by increasing temperatures above ambient. On the basis of the results in Chapter 4, Amberley seed orchard is not the most strobilus-productive site in New Zealand. Sites that have warmer summer temperatures were shown to carry more strobili. Thus it was expected that by increasing the temperature during the summer, strobilus number would have increased. The main warming treatment, the polyethylene house did create a warmer environment; its mean temperature was 20.0°C, which was some 5 °C warmer then ambient. The mean maximum temperature was 30.4°C. However, the top strobilus producing sites in Chapter 4 (10 sites) and Chapter 5 (6 sites), respectively, had long term mean daily temperatures during January, February and March of 16.9°C and 18.7°C respectively. The mean maximum temperatures at those sites for the same months were 21.8°C and 23.7°C. Clearly, at some of the top strobilus producing sites sampled, the long term maximum temperature during the summer was some 9°C cooler than that recorded in the polyethylene house. Thus it is likely that strobilus production was inhibited in this study because the temperature elevations were too great.

It is interesting to consider the report on radiata pine strobilus production at Kulani Camp in Hawaii, perhaps the most tropical latitude in which radiata pine has been successfully grown (Lanner, 1966). Here receptive strobili were reported to be present at several different times of the year. The mean maximum temperature of the warmest month (August) there is 18.7°C, supporting the perception that the temperatures in the polyethylene house were too high for

reproductive development in radiata pine. It is also interesting to note that at the Kulani camp site the long term mean minimum temperature of August is 5.6°C colder than that for the top strobilus-producing site Ngunguru in the survey study for this thesis; which had a mean minimum February temperature of 15.5°C. However, in Hawaii the temperature differential between the mean temperature of the warmest and coldest months is 2.9°C; with a comparable value for Ngunguru being 8.0°C. Thus while the Hawaii site is not warmer in absolute terms than the warmest parts of New Zealand, it has much less seasonal variation.

Temperature data obtained from Sweet (1981) for the second northern most natural stand of radiata pine at Ano Nuevo in California were considered as it was thought that they may be indicative of the environment in which radiata pine evolved. Further, this Californian site is at a similar latitude in the Northern Hemisphere to some North Auckland sites in the Southern Hemisphere where highest numbers of strobili in New Zealand are carried. Although the closest meteorological stations are at different altitudes from the stands, the temperatures for the warmest and coldest months of the year were comparable for Ano Nuevo and the New Zealand sites (see Appendix G). It is interesting to note that for both the Ano Nuevo and New Zealand sites that the temperature differential between the warmest and coldest months was over three times that for the Hawaii site. And the mean maximum temperature for the warmest month at Ano Nuevo was 18.2°C again suggesting that the temperatures in the polyethylene house were well above those under which radiata pine may have evolved. It is also interesting that the site temperatures for the top strobilus-producing sites in New Zealand are comparable with those of a site where one of the major native stands is growing.

Considering winter cold was shown to reduce the number of strobili emerging at anthesis, it was unexpected to find that the heated glasshouse treatment completely prevented strobilus development. The 2 factors potentially implicated were seasonal and diurnal temperature variability, both of which were considerably less than that outside.

Although the meteorological data from the plantation of radiata pine in Hawaii do not show major seasonal variability in temperature (see Appendix F), the decline in minimum temperature from the hottest to the coolest month shows a progressive drop of 4.6°C. Perhaps the critical factor preventing strobilus development in the glasshouse treatment was not the amount of chilling but that the winter cooling was reversed before it had been completed.

Overall, the findings of these 2 experiments support the model in Chapter 4. In both experiments, reducing the temperature at which trees were growing, reduced strobilus number at anthesis. While it was unfortunate that strobilus numbers could not be increased by increasing temperature, it is believed that with knowledge gained from these experiments, this could be done successfully in future experiments.

CHAPTER 9

THE IMPACT OF EARLY AND LATE SUMMER IRRIGATION ON NUMBERS OF EMERGENT STROBILI

A. INTRODUCTION

There are numerous references to irrigation effects on strobilus production and seeding in conifers (see Chapter 2). One broad thrust of that material is to suggest that the beneficial role for irrigation is to increase crown growth, and thus increase the number of potential strobilus sites.

But other literature suggests that the timing is critical. That water stress at the time of differentiation promotes strobilus production; and that conversely irrigation at that time reduces it. A typical reference reporting a reduction in strobilus number through irrigating at the time of seed-cone bud differentiation is that of Jett (1983), working with loblolly pine.

In Chapter 4, soil water status around the time of seed-cone bud differentiation in the summer was found to be significantly negatively correlated with strobilus numbers, and a significant independent variable in the model; although it only accounted for around 6% of the variability in between-site strobilus production patterns.

Irrigation during the late spring, at the time of seed fertilisation and rapid cone growth has been found beneficial for seed yield in seed orchard clones of *Pinus radiata* (Setiawati, 1994). However, it was unclear whether irrigation over that period impacted on the number of seed-cone buds initiated/determined in the following year.

Considering that there is limited published information on the impact of water stress in *Pinus radiata* seed orchards, it was considered appropriate to: (i) experimentally verify the effect of this variable in the strobilus production model; and (ii) establish whether in seed orchard clones, summer irrigation impacts on female strobilus production the following year.

A further aspect of the second study was to establish how long into the summer can irrigation be applied and potentially increase seed yield without compromising the next year's crop of strobili. Thus an irrigation schedule was designed where groups of ramets were irrigated for one through to five months, starting in November (late spring).

B EXPERIMENTS

1. IRRIGATION POT TRIAL

1.1 MATERIALS AND METHODS

1.1.1 Experimental Design

A 3×3 factorial experiment was conducted during the later part of the 1992/1993 growing season using potted grafts of *Pinus radiata*. This comprised 3 clones (268-54, 268-514, 268-109) and 3 levels of irrigation (well irrigated, moderately irrigated, non-irrigated). There were 10 replicate grafts in each of the 9 treatment groups, giving 90 grafts in the complete experiment.

1.1.2 Clonal Material

Grafts were potted and grown as described for those used in experiments reported in the previous experimental Chapters 7 and 8. The grafts were in their first year after establishment.

1.1.3 Irrigation Regime

The irrigation treatments were started on the 1st of January 1993 and were stopped at the end of March 1993.

The irrigation regime was as follows:

1. Well irrigated - pots were irrigated every second day.

2. Moderately irrigated - pots were irrigated once per week.

3. Control - pots received only natural rainfall.

None of the pots were covered; and so regardless of irrigation treatment they were all watered by any natural rainfall.

1.1.4 Needle Water Potential Measurements

On the 13th of February 1993 and 17th of February 1993 the water potential of needles was measured using a needle pressure bomb, as described in Chapter 3. Five needles (n=5) were sampled in each treatment group. Each needle was harvested from close to the terminal bud of a separate graft. Sampling and water potential determination was done on each of the above dates around noon time. Both days were sunny.

1.1.6 Gibberellin $A_{4/7}$ Application

As for the transfer experiment in Chapter 7, to ensure adequate strobilus initiation in 1-year-old grafts, all grafts were treated with $GA_{4/7}$. Each graft received a dose of 0.5mg of crystalline $GA_{4/7}$ in 95% ethanol, via a bud application made on the 17th of February 1993 after the needle water potential measurements had been made.

1.1.7 Assessment

In September 1993, following the time of anthesis, the total numbers of strobili, branches and latent buds in the first cycle of annual growth were counted.

1.1.8 Statistical Analysis

Statistical analysis was done using PROC GLM and Fisher's protected LSD test (SAS Institute, 1987). A factorial analysis of variance (ANOVA) was used to test all the main and interaction effects as a result of irrigation treatments across clones. The F tests for all effects discussed are significant at the 5% level. On the basis of the Fisher's protected LSD test, significant differences are at the 5% level. Data are presented as means with conventional LSD symbols. Variance quoted in the text is ±SE.

1.2 RESULTS

1.2.1 Emergent Strobili

These results are presented in Table 9.1.

Irrigating grafts around the time of seed cone bud differentiation decreased the number of emergent strobili and in turn the total number of long shoots carried by grafts at the time of anthesis. Regardless of clone, irrigated and moderately irrigated grafts carried fewer strobili than control grafts. The irrigation treatments had little impact on the numbers of latent bud or branches produced by grafts within the whorl of strobili; numbers of these shoot components did, however, vary between clones.

1.2.2 Soil Water Stress Integral

The soil water stress integral of the pot media in the control treatments (for February 1993 and March 1993) was estimated by the soil water balance model (Appendix B) to be -59.6 MPa. The potting mix had a volumetric water holding capacity (at field capacity) of 0.75 cm^3cm^{-3}. At wilting point the volumetric water content was 0.65 cm^3cm^{-3}. These values were determined by the pressure plate (field capacity) and tension table (wilting point) methods (Soil Science Department, Lincoln University).

1.2.2 Needle Water Potential

These results are presented in Table 9.2.

In February the water potential of needles in control grafts was lower than that of grafts that were irrigated or partially irrigated . Regardless of water treatment grafts were more water stressed on the 17th of February 1993 than the 13th of February 1993.

Table 9.1

The effect of irrigation on mean numbers of reproductive and vegetative components in the first annual growth cycle of potted grafts. The data are presented as mean values per graft.

Irrigation	Emergent strobili	Branches	Latent buds	Long shoot bud components
Control	[1]4.2[a]	1.8[a]	2.7[a]	8.8[a]
Irrigated	2.3[b]	1.6[a]	2.8[a]	6.7[b]
Partial irrigation	3.9[a]	1.6[a]	3.1[a]	8.6[a]
[2] Calculated probability level (Pr>F)				
Clone	0.0217	0.0530	0.0038	0.0005
Irrigation	0.0001	0.3936	0.2895	0.0004
Clone × Irrigation	0.1032	0.0273	0.3927	0.0001

[1] Values without a common letter differ at the 5% level as per a Fisher's Protected LSD test.

[2] Significance testing was carried out on $\log_e$-transformed data.

Table 9.2

The water potential of needles in potted grafts at two dates in February. Assessments were made randomly with respect to clone. The data are presented as mean values per graft ±SE.

Date	Needle water potential (MPa)		
	Irrigated	Partial irrigation	Control
13 February	-0.52±0.03	-0.48±0.04	-0.97±0.05
17 February	-0.70±0.02	-0.71±0.02	-1.33±0.05

1.3 DISCUSSION

The rationale for undertaking these water stress studies was to verify under experimental conditions the effect of soil water status during the time of seed-cone bud differentiation on the number of emergent strobili at the time of anthesis. In essence to validate experimentally the findings of the strobilus model in Chapter 4.

Irrigating grafts in pots during January, February and March suppressed strobilus production. This result is in agreement with the findings of the model in Chapter 4, that sites with soil that was more water stressed (i.e., had a larger negative soil water integral value) tended to carry more strobili. The soil water stress integral calculated for the control pots in this experiment was -59.6 MPa which is similar to the mean value for the highest 10 strobilus-producing sites in Chapter 4. The mean value for the first ten sites was -63.1 MPa.

The mean number of strobili carried per whorl by the 1-year-old grafts in the control treatment was regarded as very high in terms of all the experiments in this project. Considering that the water stress level in the pots was comparable to that of soils at the top sites in Chapter 4, it is reasonable to suggest that water stress, may in part, have promoted strobilus production in this experiment.

This result is consistent with much of the published literature that has implicated soil water stress during the growing season, generally along with warm temperatures, with increased strobilus production.

The mechanism by which water stress treatments promote strobilus production is largely unclear (see Chapter 2). One explanation is that water stress causes a build up of more non-polar gibberellins which are thought to be associated with reproductive activity (Webber *et al.*, 1985). Another proposal is that water stress modifies the growth rate of the lateral buds (long shoot buds) compared to that of the apical meristem. This in turn results in more of these buds switching to seed-cone buds (Ross *et al.*, 1984).

The irrigation treatments in this experiment commenced on the 1st of January 1993 and finished at the end of March 1993. Subject to any qualification from the work of Dickson, Riding and

Sweet (1994) it can be assumed that the treatments covered the period of long shoot differentiation, and possibly also included long shoot initiation (see Appendix A). They certainly coincided with the time at which gibberellin application is effective. While gibberellins have been shown to increase both the number of strobili and also the number of total long shoots, the irrigation treatment in this experiment had the reverse effect. Irrigation reduced the total number of long shoot bud components, as well as strobili.

Considering that the primary reason for this trial was to confirm the findings of the model (Chapter 4) it was considered appropriate to conduct water stress experiments on trees growing in pots, and under field conditions. The pot trial served as a preliminary study, to confirm that water stress was likely to be involved with the differentiation of emergent strobili in *Pinus radiata*. Subsequently an irrigation trial was conducted in a seed orchard situation, and that will be reported in the next section of the chapter.

2. IRRIGATION FIELD TRIAL

2.1 MATERIALS AND METHODS

2.1.1 Site

This trial was conducted at Amberley seed orchard, Canterbury, South Island, New Zealand; from the 1st of November 1993 until 31st of March 1994. It was laid down in the 1991-planted meadow orchard comprising grafted ramets. The experimental design was governed by the clonal-block plantings in the orchard. The grafts in this trial were 1 year older than those used in the irrigation pot experiment.

2.1.2 Trial Design

The experiment was conducted according to a split plot design with a randomised arrangement of the subplots (sub-treatments); a combination of 6 irrigation times (i.e., watering for 0,1,2,3,4 or 5 months) (Figure 9.1). The main plots were 3 clones (268-109, 875-76, 268-54). Within each clone 6 rows of ramets were selected, one for each irrigation subplot. Within each row 10 replicate ramets were randomly selected. The 18 treatment groups, each with 10 replicate ramets, gave a total of 180 ramets in the complete experiment.

2.1.3 Irrigation System

This comprised a thin-walled trickle irrigation polythene pipe, "Netafim" button drippers (water emitters) (Fruitfed Supplies Ltd) and an "Onga" pressure pump (Canterbury Ground Water Ltd).

The pipe layout comprised two different sizes of pipe, namely a feeder pipe (30mm) and lateral pipe (25mm). The feeder pipe carried the water from the supply tank to each of the rows of ramets to be irrigated. Along each of these rows the lateral pipe was laid down. Each lateral line was connected into the feeder pipe.

Along the length of each lateral line, two button drippers were inserted adjacent to each ramet; they were positioned around 100mm either side of each ramet stem (see Plate 9.1).

During the experiment the irrigation system was switched on for 2 hours per day. It operated at a pressure of 0.21 MPa. At this pressure each button dripper was specified to deliver 2 litres of water per hour. In total each irrigated ramet received around 8 litres of water per day.

2.1.4 Irrigation Treatments

Of the 6 "irrigation" treatments, one was a non-irrigated control. Each of the other 5 was irrigated for 1, 2, 3, 4 or 5 months; starting in November 1993. At the end of each month one lateral irrigation line per clone was disconnected from the feeder line. It follows that by the beginning of March 1994 only the ramets in the March irrigation treatment (within each clone) were still being irrigated.

In order to avoid the lateral movement of water between irrigation subplot treatments, at least one row of ramets was left between plots. The rows in the 1991-planted meadow orchard at Amberley are planted 2 metres apart. Thus the distance between irrigation plots was at least 4 metres.

Figure 9.1

Diagram of Irrigation Trial Layout

CLONE 268-54 - MAIN PLOT

IRRIGATION	RAMET NUMBER									
	1	2	3	4	5	6	7	8	9	10
CONTROL	#	#	#	#	#	#	#	#	#	#
1 MONTH	#	#	#	#	#	#	#	#	#	#
2 MONTH	#	#	#	#	#	#	#	#	#	#
3 MONTH	#	#	#	#	#	#	#	#	#	#
4 MONTH	#	#	#	#	#	#	#	#	#	#
5 MONTH	#	#	#	#	#	#	#	#	#	#

CLONE 268-109 - MAIN PLOT

	1	2	3	4	5	6	7	8	9	10
CONTROL	#	#	#	#	#	#	#	#	#	#
1 MONTH	#	#	#	#	#	#	#	#	#	#
2 MONTH	#	#	#	#	#	#	#	#	#	#
3 MONTH	#	#	#	#	#	#	#	#	#	#
4 MONTH	#	#	#	#	#	#	#	#	#	#
5 MONTH	#	#	#	#	#	#	#	#	#	#

CLONE 875-76 - MAIN PLOT

	1	2	3	4	5	6	7	8	9	10
CONTROL	#	#	#	#	#	#	#	#	#	#
1 MONTH	#	#	#	#	#	#	#	#	#	#
2 MONTH	#	#	#	#	#	#	#	#	#	#
3 MONTH	#	#	#	#	#	#	#	#	#	#
4 MONTH	#	#	#	#	#	#	#	#	#	#
5 MONTH	#	#	#	#	#	#	#	#	#	#

1. For simplicity the subplots (irrigation) have been shown in an un-randomised form.
2. 10 ramets out of each row of 20 ramets were randomly selected; the ramets that were not selected in each row are not shown.

Plate 9.1

A view of two button drippers (water emitters) positioned adjacent to an orchard ramet used in the irrigation field trial.

2.1. 5 Soil Water Status

The soil type in the meadow orchard was a Glenmark gravelly clay loam (as per a report prepared for Rayonier N.Z. Ltd by Landcare Research Ltd).

For **non-irrigated** soil, daily water potential for the months October 1993 through to March 1994 was estimated using the soil water balance model used in Chapter 4 (see appendix B), along with the temperature, rainfall and solar radiation data collected during that time by the "Monitor" automatic weather station at the orchard. The soil water stress integral (see Chapter 4) was calculated for February 1994 and March 1994 from the daily water potential estimates of the soil water balance model.

2.1.6 Gibberellin $A_{4/7}$ Application

On the 23rd of February 1994, all ramets received a dose of 25mg of crystalline $GA_{4/7}$ via a stem injection application. The gibberellins were dissolved in 95% ethanol, and a 0.5ml of this solution was injected into a 0.5mm hole drilled at the base of each ramet.

2.1.7 Assessments of Strobilus and Branch Number

In September 1994, the number of emergent strobili produced in the first cycle of annual growth on branches and main stems of ramets across treatments was assessed. The mean number of strobili, branches and latent buds per whorl; along with the mean number of strobilus-bearing branches per ramet was calculated.

2.1.8 Statistical Analysis

Statistical analysis was done using PROC GLM and Fisher's protected LSD test (SAS Institute, 1987). A factorial analysis of variance (ANOVA) was used to test all the main and interaction effects as a result of irrigation treatments across clones. The F tests for all effects are significant at the 5% level. On the basis of the Fisher's protected LSD test, significant differences are at the 5% level. Data are presented as means with conventional LSD symbols. Variance quoted in the text is ±SE.

2.2. RESULTS

2.2.1 Mean Total Numbers of Emergent Strobili

These results are presented in Table 9.3.

Overall, irrigation had little effect on the mean number of emergent strobili per whorl. Although there was a statistically significant reduction in strobilus number when irrigation was stopped in December, logic would make it seem unlikely that this was a real result.

2.2.2 Mean Total Number of Branches and Latent Buds

Irrigation had no significant effect on the number of long shoot buds produced within whorls; or the number of branches and latent buds. Further, irrigation had no significant effect on the number of branches in the crown that produced strobili.

2.2.3 Rainfall

Refer to Table 9.4.

The total rainfall for the months November through to March was greater in 1993/94, the year of the experiment than in 1992/93. The latter year had approximately 28% more rainfall for those months, with the total rainfall recorded being 333mm.

2.2.4 Soil Water Status

The soil had a volumetric water holding capacity (at field capacity) of 0.43 cm^3cm^{-3}. At wilting point the volumetric water content was 0.11 cm^3cm^{-3}. These values were determined by the tension table and pressure plate methods (Soil Science Department, Lincoln University).

The water content of soil in the non-irrigated and irrigated treatments was calculated to establish whether the grafts being irrigated had more soil water available to them than those not irrigated. Soil was sampled to 0.30m and its volumetric moisture content determined using time domain reflectometry (T.D.R.) (0.30m rods). The readings were then converted to matric

potentials (MPa) using the root zone matric potential equation in Appendix B.

Unseasonal rainfall during the summer months at Amberley seed orchard kept the soil moist. On the 17th of February 1994 the mean soil water potential in the irrigated plots and the control (non-irrigated) plots was, respectively, -0.32 ±0.10 MPa and -1.34 ±0.04 MPa. Although there was a difference in soil water potential between the 2 treatments, clearly trees growing in soil at around -1.3 MPa are unlikely to be experiencing severe water stress effects.

The soil water stress integral estimated for both February 1994 and March 1994, using the soil water balance model, was -13.4 MPa. This is a particularly low value for this parameter (compared to values in Table 4.6, Chapter 4).

Table 9.3

The effect of irrigation commencing on the 1st of November 1993 on strobilus production by ramets at Amberley seed orchard. Control ramets were watered only by natural rainfall. The data are presented as mean values per ramet.

Date Irrigation stopped	Emergent strobili/whorl	Number of strobilus bearing shoots	Number of branches\whorl	Number of latent buds/whorl	Number of long shoot bud components
Control (no irrigation)	3.47[a]	1.89[a]	1.54[a]	0.37[a]	5.38[a]
30 November 93	3.31[a]	1.55[a]	2.06[a]	0.35[a]	5.72[a]
31 December 93	2.43[b]	1.45[a]	2.25[a]	0.20[a]	4.88[a]
31 January 94	3.54[a]	1.64[a]	1.48[a]	0.26[a]	5.28[a]
28 February 94	3.94[a]	1.76[a]	1.58[a]	0.52[a]	6.04[a]
31 March 94	3.92[a]	1.95[a]	1.62[a]	0.41[a]	5.95[a]
[2]Calculated probability level (Pr>F)					
Clone	0.0001	0.1210	0.0001	0.0001	0.0001
Irr	0.0047	0.0500	0.1742	0.4111	0.1702
Clone×Irr	0.3337	0.0165	0.0024	0.2888	0.0016

[1] Values without a common letter differ at the 5% level as per a Fisher's Protected LSD test.

[2] Significance testing was carried out on $\log_e$-transformed data.

Table 9.4

Recorded rainfall at Amberley seed orchard for the summer months November through to March inclusive for 1992/93 and 1993/94. The irrigation trial was conducted during the 1993/94 summer period.

Month	Rainfall (mm)	
	1992/93	1993/94
November	13.5	68.5
December	11.0	131.5
January	32.5	46.5
Febraury	39.0	32.0
March	16.5	54.5

2.3 DISCUSSION

The strobilus production model in Chapter 4 indicated that the numbers of emergent strobili were greater on sites which were drier than wetter sites during February and March. However, the water stress integral (an independent variable) only accounted for some 6% of the between-site variance in strobilus numbers. Thus this variable does not appear to be a key one regarding numbers of seed-cone buds beginning to differentiate. But as a finding it is comparable to most of the reports in the literature on water stress and strobilus production in forest trees.

Contrary to much of the literature, Australian researchers have reported that irrigation promotes coning in radiata pine (Griffin, Crane and Cromer, 1984). However, relative to New Zealand sites it is likely those in Australia are drier, such that growth is not easily maintained. The site at which Griffin, Crane and Cromer (1984) found a positive irrigation effect had an annual rainfall that varied between 315mm and 650mm. Their data indicated a positive response to water only when the rainfall fell below 600mm per year. The mean annual rainfall (for a 30 year period) in the Amberley area (Waipara and Sandhurst) is 729mm, and ranges between 500mm and 887mm (data obtained from N.I.W.A.). Clearly Amberley seed orchard has a higher rainfall and is likely to experience fewer droughting events than the orchard site that Griffin, Crane and Cromer (1984) conducted their irrigation trial at. The total rainfall for the 5 summer months in 1993/94 that the irrigation was run at Amberley seed orchard was 333mm.

It is probable that under extremely dry conditions irrigation maintains shoot growth rate and thus allows the opportunity for long shoot primordia initiation. Certainly, Schmidtling (1985) reported that irrigation increased strobilus production in *Pinus echinata*, and this was especially apparent during a severe drought in 1980. On the other hand Barnes and Bengston (1968) reported that irrigation of *Pinus elliotii* at an orchard site with a rainfall of 1300mm per year suppressed female strobilus production.

It is unlikely that strobilus production responds to soil water content in a linear fashion, especially across a large range of soil types and water content values. Hence it is not unexpected to find disagreement in the literature regarding irrigation effects on strobilus production.

As stated in the pot experiment the main issue in this chapter was to establish whether water stress effects in the model in Chapter 4 could be reproduced experimentally. Because of the obvious difficulties of applying water stress treatments in seed orchards which are subject to rain, the alternate approach was taken of reducing water stress by irrigation. But even this approach was non-yielding when frequent rainfall kept the soil in the non-irrigated controls wetter than desirable. The differential in soil water status between the control and irrigated plots was not sufficiently large enough to promote a water stress effect on numbers of emergent strobili.

Nevertheless, there was some indication that soil moisture was playing a role in seed-cone bud differentiation. In the field trial the mean number of strobili carried per whorl by ramets in the control treatment (non-irrigation) was 3.47 which was less than the 4.20 carried by control grafts in the pot experiment, that were subjected to greater levels of water stress. Two identical clones were used in the field trial and the pot trial, namely clones 268-109 and 268-54. The mean number of strobili per whorl carried by clone 268-109 in the field trial and pot experiment was, respectively, 2.77 and 4.60. And for clone 268-54 the mean number of strobili per whorl was 2.23 and 4.55 for the field and pot experiments, respectively. Considering the soil water stress integral for the field trial and pot experiment was -13.4 MPa and -59.6 MPa, respectively, it is suggested that the moist conditions in field trail suppressed strobilus production. This proposal is further supported by the fact that trees in the field trial were 1 year older than the ones in pots. Averaged over the orchard as a whole, a typical 2-year-old graft carries around 1.8 times the number of strobili of a typical 1-year-old graft. This was not the case, however, for the wetter 1993/1994 years at Amberley which resulted in below optimal numbers of strobili being carried by the non-irrigated control trees.

C. GENERAL DISCUSSION

Compared to the 10 most productive sites for strobilus number in Chapter 4, the soil water stress integral for the irrigation field trial was considerably less (-63.1 MPa for the 10 most productive sites compared to -13.4 Mpa for the field trial); and the number of strobili carried by ramets was less than often occurs. The results of the irrigation experiments in this chapter, along with the data in Chapter 4, indicate that the soil water stress integral is related to some extent with strobilus production levels across sites. If the value for this variable is close to -60 MPa (for February and March) it is likely that strobilus numbers will be near optimal. This statement was supported by the findings of the pot experiment where 1-year-old grafts carried high numbers of strobili per whorl.

The findings of both the experiments in this chapter support the inclusion of the soil water stress integral in the model (Chapter 4). It appears that irrigation does to some extent reduce the number of seed-cone buds that begin differentiating. However, it does require recalling that in Chapter 4 the water stress variable only explained some 6% of the between-site variance for strobilus counts. One would thus expect that it would be difficult to demonstrate such a small effect statistically.

CHAPTER 10

THE EFFECT OF SPRING GROWING CONDITIONS ON BUD AND CROWN GROWTH

A. INTRODUCTION

Shoot extension growth has frequently been implicated as a factor associated with strobilus production in conifers (see Chapter 2). In *Pinus*, vegetative growth has been reported to influence the morphogenesis of generative organs. (Varnell, 1976; Bollmann, 1983; Ross, 1991; Bonnet-Masimbert and Doumas, 1992).

Generally in woody plants there exists a negative relationship between shoot growth and "flowering" (Jackson and Sweet, 1972). Examples of this in *Pinus* lie in the regular annual coning of old trees which are no longer making vigorous vegetative growth. This appears to be relatively independent of site. And so-called "distress crops" are regarded as the ultimate example. However, although restricted vegetative growth during bud initiation may favour reproductive activity, it is acknowledged that in younger trees there is a requirement for vegetative growth during other times of the growing season.

Bollmann and Sweet (1976) observed that the more cycles of growth *Pinus radiata* initiates during the growing season the more opportunity there is for seed-cone buds to be differentiated. Similarly, the more vigorous an individual branch growth is within the crown the more axillary long shoot primordia are likely to be initiated, thus again increasing the opportunities for seed-cone buds to form.

Some orchardists use cultural treatments to change the growth of ramets over time in an attempt to promote strobilus production. For example, the use of fertilisers to develop crown growth and increase the number of branch sites for initiating strobili. Others use release treatments to increase the growth of individual branches, or girdling/strangulation to keep carbohydrate levels up in the crown.

It has been clearly demonstrated through experiences of the *Pinus radiata* seed orchards in New Zealand that site conditions impact on the amount of branching and crown growth (see Chapter 1), and thus in turn numbers of strobili.

The multiple regression model in Chapter 4 selected a variable G_r which is a measure of the amount of temperature and rainfall across sites during the spring. This variable was found to be highly correlated with numbers of emergent strobili across a range of sites. It follows that the amount of growth during spring may influence the number of long shoot buds initiated and in turn numbers of emergent strobili at anthesis. To that end it was considered appropriate to test the effect of growing conditions, particularly in the spring, on strobilus production in clonal grafts in *Pinus radiata.*

The overall intent of the experiment described in this chapter was to use treatments that modified shoot growth to verify the importance of this phenomenon on strobilus production in clonal grafts of *Pinus radiata.*

B. OBJECTIVE

The intent of this experiment was to establish whether warm moist conditions during the period prior to seed-cone bud initiation increased shoot and bud size, such that more seed-cone buds were differentiated, and hence a greater number of emergent strobili were carried at anthesis. It was intended to increase the size of the terminal buds on the main stem such that a greater number of long shoot primordia were initiated and thus increasing the opportunity for seed cone buds to be differentiated. The main stem shoot was the only shoot on the 2-year-old grafts that had attained a size such that it could carry strobili.

C. MATERIALS AND METHODS

1.0 Site

This experiment was a pot trial conducted at Amberley seed orchard and the glasshouse complex at the University of Canterbury.

1.1. Experimental Design

The trial was a 3×3 factorial experiment conducted during the early part of the 1993/1994 growing season. This comprised 3 clones (268-54, 268-514, 268-109) and 3 spring growth (pre-long shoot primordia initiation) treatments. Within each of the 9 treatment groups there were 9 replicate grafts giving 81 grafts in the complete experiment.

1.2 Material

2-year-old potted grafts, that were propagated and grown as described in Chapter 7, were used in the experiment.

1.3 Spring Growth Treatments

As stated, there were 3 spring treatments where grafts were:

1. Irrigated and kept in a glasshouse heated to 20°C from September 1993 to November 1993, at the University of Canterbury.
2. Water-stressed and kept at Amberley seed orchard.
3. Kept at Amberley seed orchard and only irrigated when natural rainfall was inconsistent.

Rainfall was kept from the soil of the grafts in the water stress treatment by enclosing each pot in a sealed plastic bag, as described in Chapter 8 for the cooling treatment.

At the end of November 1993 all grafts were re-grouped at the same location in Amberley seed orchard; the plastic bags were removed from those in the water stress treatment.

1.4 Vegetative Growth Measurements

The growth grafts had made in each of the treatments was measured in January 1994. This involved measuring needle growth, lateral branch growth, terminal and lateral bud diameter and graft height.

Ten fully extended needles were sampled from each of the 9 replicate grafts within each treatment group. Using a Li-Cor 3100 leaf area metre the one-sided surface area of each needle (cm^2) was measured. Then assuming the needle cross-section to be a sector of a circle, the ratio π was used to convert the one-sided measurements (of leaves) to total surface area of pine needles (see Grace, 1987). While concern has been expressed about the value of the π conversion factor in such calculations for non-flat leaves (Chen and Black, 1992), it was considered more important to look for relative rather than absolute differences between treatments in the needle area data. It was unlikely that these data were going to be used in detailed growth analysis studies or photosynthetic calculations, in which case it would have been more appropriate to calculate needle area from length and volume or dry weight and density measurements (Beets, 1977).

Following area measurements, needle dry weight was determined after drying in an oven for 24 hours at 60°C.

Bud measurements were made on every graft. The terminal and 3 lateral branch buds were measured using a pair of calipers. At this time the height of each graft was recorded. Finally, the length of 3 lateral branches per graft was measured.

1.5 Strobilus Counts

In September 1994, following the time of anthesis, the total numbers of strobili, branches and latent buds in the first cycle of annual growth were counted.

1.6 Gibberellin $A_{4/7}$ Applications

On the 23rd of February 1994 all ramets received a dose of 25mg of crystalline $GA_{4/7}$ via a stem injection application. The gibberellins were dissolved in 95% ethanol, and a 0.5ml of this solution was injected into a 0.5mm hole drilled at the base of each ramet.

1.7 Statistical Analysis

Statistical analysis was done using PROC GLM and Fisher's protected LSD test (SAS Institute, 1987). A factorial analysis of variance (ANOVA) was used to test all the main and interaction effects as a result of growth treatments across clones. The F tests for all effects discussed are significant at the 5% level. On the basis of the Fisher's protected LSD test, significant differences are at the 5% level. Data are presented as means with conventional LSD symbols. Variance quoted in the text is ±SE.

D. RESULTS

These are presented in Table 10.1 and Table 10.2.

Grafts grown in the glasshouse did have larger needles, but their terminal buds were no larger in diameter than those of control grafts kept at Amberley seed orchard. However, the length of the second order lateral branches was significantly increased by the glasshouse conditions. Compared to the control treatment, the glasshouse treatment increased the length of the lateral branches by 5.1% and the diameter of their buds by 16.6%. These lateral branches were not sufficiently large enough, however, to initiate and carry strobili. The glasshouse conditions also significantly increased graft height growth.

Both the interception of solar radiation and photosynthesis depend on the surface area of the foliage. The needle growth of the glasshouse grafts was greatly increased compared to that of the control grafts. The mean glasshouse needle dry weight, area and length was, respectively, 1.55, 1.63 and 1.63 times greater than that of the Amberley control treatment.

In the short term there was no indication that the increased growth rates in the glasshouse material led to increased strobilus production. In fact they produced significantly fewer strobili (See Table 10.2). What was very apparent was that spring growing conditions impacted on the number of branches per whorl. Both the glasshouse and the control grafts produced more branches per whorl than the stressed grafts, and apart from the glasshouse material the increased branch number did not result in a parallel reduction in the numbers of emergent strobili.

Grafts grown in the glasshouse for part of the spring made more growth compared to those kept at Amberley, either control or water stressed. The needles, branches and lateral buds in the glasshouse treated grafts were larger compared to those in the other treatments.

Table 10.1

The effect of early season growing conditions (September 1993 to November 1993 inclusive) on the size and weight of graft shoot components. The data are presented as mean values per graft.

Spring growth treatment	Needle dry weight (g)	Needle area (cm^2)	Needle length (cm)	Graft height (m)	Lateral branch length (cm)	Lateral bud diameter (mm)	Terminal bud diameter (mm)
University Glasshouse	0.14[a]	40.5[a]	14.2[a]	0.8[a]	16.6[a]	3.5[a]	5.6[b]
Amberley stressed	0.05[c]	9.1[c]	4.5[c]	0.7[b]	11.2[b]	1.9[c]	4.4[c]
Amberley control	0.09[b]	24.8[b]	8.7[b]	0.7[b]	15.8[b]	3.0[a]	7.5[a]
[2] Calculated probability level (Pr>F)							
Treatment	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Clone	0.0042	0.0051	0.0591	0.0019	0.7386	0.0224	0.1012
Treatment×Clone	0.6550	0.8681	0.9778	0.5929	0.2375	0.2168	0.2693

[1] Values without a common letter differ at the 5% level as per Fisher's Protected LSD test.

[2] Significance testing was carried out on $\log_e$- transformed data.

Table 10.2

The effect of early season growing conditions (September 1993 to November 1993 inclusive) on the numbers of emergent strobili, branches and latent buds per first annual cycle of growth. The data are presented as mean values per graft.

Spring growth treatment	Strobili/whorl	Branches/whorl	Latent buds/ whorl	Total shoot components/ whorl
University Glasshouse	1.09[b]	5.52[a]	1.57[b]	8.18[a]
Amberley stressed	2.30[a]	0.78[c]	3.69[a]	6.77[b]
Amberley control	2.71[a]	2.21[b]	3.00[a]	7.92[a]
[2] Calculated probability level (Pr>F)				
Treatment	0.0035	0.0001	0.0005	0.0274
Clone	0.0233	0.3492	0.2303	0.0134
Treatment×Clone	0.1205	0.5809	0.7393	0.1071

[1] Values without a common letter differ at the 5% level as per Fisher's Protected LSD test.

[2] Significance testing was carried out on $\log_e$-transformed data.

E. DISCUSSION

This study investigated the effect of shoot growth early in the growing season on numbers of emergent female strobili at anthesis.

The rationale of the experiment was to verify the significance of the spring growth variable (G_r) in the strobilus model (Chapter 4). This variable although it only accounted for 4% of the unexplained variance indicated that strobilus production was to some extent dependent on site temperature and rainfall conditions during the early part of the growing season. Obviously, these conditions influence the growth rates of shoots during this time, which has been associated with the number of seed-cone buds that may begin differentiating (Griffin, Crane and Cromer, 1984). Tosh and Powell (1990) showed that cone production in *Larix laricina* trees was positively correlated with rapidity of crown production, which was related to site conditions.

In the short term increased growth rate following a 6 week period in the glasshouse did not translate to increased strobilus production; in fact it caused a significant decrease compared to the control treatment. However, it did lead to increased branches per whorl. In the longer term this would have an effect on strobilus production by increasing the number of strobilus-producing sites within the crown. It is likely that this indirect growth effect on strobilus production is the main reason why the growth variable G_r was found to be a significant predictor in the strobilus production model (Chapter 4). It follows that if branch vigour was comparable, trees with higher numbers of branches per whorl could carry more strobili than those with fewer.

Compared to the water stress treatment the control treatment produced significantly more branches and strobili, thus indicating that in the short term, branches can be produced without compromising strobilus production.

The key to the explanation lies in the difference between this short-term experiment, and the model in Chapter 4 which was based on trees which have been growing in a given climate for 10-12 years.

The indirect effects of crown growth on strobilus production are thought to explain why some cultural treatments such as ameliorative fertiliser applications enhance coning in some conifer

seed orchards (Prof. C.B. Davey, pers. comm.). Similarly, early summer irrigation has been found to be beneficial for female strobilus production in a *Pinus echinata* seed orchard in Arkansas (Schmidtling, 1985); probably by increasing the number of strobilus-producing sites in the crown. In 2 years out of 3, early season irrigation promoted strobilus production. The only year that it did not was in the first year when treatments began. Although limited data was supplied in this reference it seems likely that the spring irrigation treatments impacted on the subsequent years crop of strobili rather than the current one. Indeed this may be the case for any treatment that promotes early season shoot growth.

The results of the current experiment would support the view, that the increased branching due to the glasshouse treatment would not be reflected in a heavier strobilus crop until those branches made sufficient growth and development to become capable of initiating long shoot primordia and carrying strobili. Another example illustrating the occurrence of a lead-time for growth effects to impact on strobilus production was reported by Silen (1973b) who found that shading only began to have a negative effect on strobilus production in *Pseudotsuga menziesii* in the second year of treatment.

In summary, in terms of seed orchard site selection it is likely that during the spring/early summer site conditions need to be such that ramets make some vegetative growth, not only for their survival but also to ensure some reproductive development. However, it is clearly undesirable to have vigorous vegetative growth throughout the whole growing season as this brings about management problems and may compromise strobilus production. Ideally at a site, there should be a balance between the levels of vegetative and reproductive growth. It is likely that if a site is meeting the temperature and soil moisture criteria for seed-cone bud differentiation during the later part of the summer, that these conditions will restrict vegetative growth.

The findings of this chapter confirm the significance of the inclusion of the G_r variable in the strobilus production model (Chapter 4), in the sense that moderate branch development is necessary for the long term production of strobilus formation sites in the crown.

CHAPTER 11

THE EFFECT OF NITROGEN-BASED FERTILISERS ON STROBILUS PRODUCTION

A. INTRODUCTION

The relationship between levels of cone and seed production, and fertiliser application, as reported in the literature, is a complex one. It is likely that several factors are confounded, but seldom is that made clear.

Firstly, because fertiliser application normally leads to increased vegetative growth, its reproductive effect can be indirect. That is, it can be the result of a larger crown providing more sites for strobilus initiation. Or alternatively the effect can be a direct one, with mineral nutrient additions directly affecting strobilus initiation. Seldom does the literature explore whether the effect was direct or indirect.

Secondly, it could be expected that the initial fertility of the soil would influence the nature and magnitude of any fertiliser response. But again, data on initial soil nutrient status, and its status for the species involved, is seldom presented in published studies.

Thirdly, with regard to nitrogen, there is literature indicating that the form (specifically nitrate or ammonium) in which it is applied is important (Ebell, 1972; Robinson, 1979). That literature is not consistent with respect to the most appropriate form, complicating the understanding of issues further.

The research presented in Chapter 4 of this thesis did not attempt to equate mineral nutrient levels with the numbers of strobili at anthesis across a range of sites. Firstly, it was not readily possible financially or logistically to determine nutrient levels on such a scale; but secondly the evidence from correlating strobilus number with soil class and texture and likely phosphate (citric soluble) levels did not indicate the likelihood of a strong correlation.

Despite that, there is a valid question for seed orchard managers to ask regarding fertiliser application. Such a question says: "accepting that my seed orchard site is properly selected on a climatic rather than a soil nutritional basis, is there still scope to increase the numbers of emergent strobili by fertiliser application"?

In New Zealand the "critical levels" of the various elements for health and vegetative growth of radiata pine have been defined for a number of years (Raupach, 1967; Will, 1978; Will, 1985). All existing seed orchards have had foliage analysis, and subsequent fertiliser application carried out to ensure that levels of all significant and trace elements exceed those critical levels (New Zealand Seed Orchard Research Group members, pers. comm.). That practice, which is aimed more at optimising health than cone production, is expected to continue in all new orchards.

If mineral nutrient levels are well above critical ones, then it is unlikely that their further application will substantially increase vegetative growth, and thus increase coning indirectly. The intent of any fertiliser application would thus have to be to affect either strobilus initiation or development directly. Amongst mineral nutrients, the only one which appears to have this potential is nitrogen (Ebell and McMullin, 1970; Griffin, Crane and Cromer, 1984; Fogal *et al.*, 1994), but N application has been thoroughly tested on radiata pine in New Zealand by Sweet and Hong (1978) with no consequent increase in strobilus number.

Annual nitrogen applications to seed orchards, however, are very widely (and supposedly successfully) used in a number of seed orchards overseas, and New Zealand managers keep questioning the past New Zealand nil result findings. Because the Sweet and Hong (1978) study was carried out on volcanic soils in the central North Island, and because that area has been largely superseded for new seed orchards, there may be an argument to re-explore the effectiveness of nitrogen application at the time of long shoot primordia initiation in meadow orchards. With strong pressure from managers in the Seed Orchard Research Group, the study reported in this chapter was thus undertaken on 3 separate orchards. Each orchard had a different soil type and past fertiliser history.

B. MATERIALS AND METHODS

1. Seed Orchard Sites

A nitrogen fertiliser trial was replicated across three seed orchard sites in New Zealand. Two of these were in the North Island at Te Teko and Matakana while the third was at Amberley in the South Island (see Table 11.1 and Figure 1.3).

Table 11.1

Seed orchard location, altitude and soil type

Orchard site	Altitude (m)	Latitude	Longitude	Soil Texture
Amberley	28.0	43°10'S	172° 20' E	Gravelly clay loam
Te Teko	8.0	38° 02'S	176° 49' E	Volcanic ash
Matakana	4.0	37° 35'S	176° 12' E	Sand

2. Soil Type and Previous Fertiliser History

An outline of soil type and previous fertiliser history of each site is given below. On none of the 3 sites is fertiliser applied on an annual basis. Further, no N fertilisers had been applied at any of the sites for more than 5 years.

2.1 Amberley

The soil was classified as a Glenmark gravelly clay loam.

Nutrient analysis was carried out on needles sampled from 5 clones shortly before laying out the trial at this site. 3 of the 5 clones were those selected for subsequent treatment. Sampling and analysis procedures were carried out as outlined in Will (1985).

2.2 Te Teko

The soil was classified as a central recent soil from volcanic ash (Tarawera) (Soil Bureau Bulletin No. 26). The texture is water sorted volcanic ash/sand (Tasman Forestry Ltd, pers. comm.).

An application of diammonium phosphate (at a rate of 250kg ha^{-1}) was made to the trial site in the first year (1991) grafts were established. In 1985, the site received an application of copperised-superphosphate with boron at a rate of 300kg ha^{-1}.

2.3 Matakana

The soil was predominantly sand with little organic matter. It was classified as a central yellow brown sand (Foxton and Pinaki) (Soil Bureau Bulletin No. 26).

In the first year of establishment each ramet received an application of 30 g of "Magamp", a magnesium based fertiliser. Later in the spring of the establishment year "Nitrophoska" (12-10-10 NPK) was applied at a rate of 100g per ramet.

3. Trial Design and Material

Following discussions with the seed orchard managers the trial was established at each of the three orchard sites in February 1993.

The trial design at each orchard was a factorial incorporating 4 N-treatments and 4 clones. Because it was not possible to treat the same clones at Te Teko as at Amberley and Matakana, each site is regarded as a separate experiment. In each experiment there were 12 replicate ramets for each treatment and clone, giving 192 ramets in total. The age of the ramets and stocking rate for each orchard are presented in Table 11.2.

Table 11.2

Clone, year of establishment and stocking rate at each orchard site

Orchard site	Clone	Year of planting	Stocking rate (Stems ha^{-1})
Amberley	268-109 268-54 268-65 875-76	1991	3300
Te Teko	268-315 268-530 875-293 880-656	1991	2000
Matakana	268-109 268-54 268-65 875-76	1991	500

4. Fertiliser Treatments

There is some thought that strobilus production in pines is dependent on the N-form applied (Prof. C. B. Davey, pers. comm.); possibly related to the efficacy of the enzyme nitrate reductase which converts nitrate to ammonium. In order to address this issue the 3 fertilisers used in this study covered the spectrum of N-forms. Within treatments individual ramets were treated with either predominantly ammonium (Urea - $(NH_2)_2CO$) or nitrate (KNO_3), or a mixture of those N-forms ($CaNH_4NO_3$).

The constituents of three fertilisers compounds used (see Cornforth and Sinclair, 1984) were:

1. $CaNH_4NO_3$ - N (27%); Ca (8%).
2. KNO_3 - N (14%); K (39%).
3. Urea - N (46%).

Thus the fertiliser treatments were:

1. Control - no fertiliser
2. $CaNH_4NO_3$
3. KNO_3
4. Urea

At all sites fertiliser treatments were applied at an equivalent rate of between 0.10 kg and 0.15 kg elemental N per ramet. This equates to around 400 kg N ha^{-1} for an orchard stocked at 2666 ramets ha^{-1}. This rate per hectare was selected on the basis of a memorandum (Re: Seed orchard fertilisation) from Dr J.B. Jett and Prof. C.B. Davey of the Department of Forestry, North Carolina State University. The area fertilised around each ramet equated to the size of its root plate. Ramet selection and fertiliser application at the 2 North Island sites were carried out by the respective seed orchard managers.

The fertilisers at each orchard were applied in mid-February 1993. The soil moisture at all sites was low at the time of fertiliser application. Thus there was concern that the dissolution of the fertiliser powders into the soil would be slow, increasing the chances of losing N by volatilisation. At the North Island sites this problem was overcome by using a water tanker and watering the fertiliser into the soil at the time of application. At Amberley, however, applications were able to be made during the time light rain was falling.

5. Gibberellin $A_{4/7}$ Application

In mid- February 1993, all ramets received a dose of 25mg of crystalline $GA_{4/7}$ via a stem injection application. The gibberellins were dissolved in 95% ethanol, and a 0.5ml of this solution was injected into a 0.5mm hole drilled at the base of each ramet.

6. Assessments

The total number of branches per ramet carrying emergent strobili; and the number of strobili per whorl were counted at all orchards. Assessments at Matakana and Te Teko were made by orchard managers.

7. Statistical Analysis

Statistical analysis was done using PROC GLM and Fisher's protected LSD test (SAS Institute, 1987). A factorial analysis of variance (ANOVA) was used to test all the main and interaction effects as a result of fertiliser treatments across clones at each individual orchard site. The F tests for all effects discussed are significant at the 5% level. On the basis of the Fisher's protected LSD test, significant differences are at the 5% level. Data are presented as means with conventional LSD symbols. Variance quoted in the text is ±SE.

C. RESULTS

1. Amberley Foliage Analysis

Amberley foliage analysis data are presented in Table 11.3.

At that site all elements analysed in each clone had satisfactorily key nutrient levels, prior to N fertiliser application. The mean clonal N concentration was 23% above the critical level, as per Will (1985).

2. Strobilus Counts

Strobilus counts are presented in Table 11.4.

At Te Teko and Matakana the fertiliser treatments did not significantly effect numbers of emergent strobili at the time of anthesis.

At Amberley differences were significant, with Urea and $CaNH_4NO_3$ significantly reducing numbers of strobili relative to KNO_3 and the control. Compared to the control, the $CaNH_4NO_3$ and Urea treatments were, respectively, 53.7% and 57.9% lower for numbers of strobili per ramet. A similar pattern occurred regarding numbers of strobili per whorl; with $CaNH_4NO_3$ and urea treatments reducing mean numbers of strobili by 38.7% and 32.2%, respectively.

Across all orchards only clonal effects were highly significant. Comparing Amberley and Matakana, which were comparable clonally and in terms of age, Matakana had an average of more than twice as many strobili per ramet.

Table 11.3

Foliage analysis Amberley seed orchard - 1993

Clone	N(%)	P(%)	K(%)	Mg(%)	Ca(%)	B(ppm)
268-109	1.7	0.2	1.2	0.2	0.2	17
268-622	1.8	0.2	1.1	0.1	0.3	27
268-54	1.9	0.2	1.2	0.1	0.2	19
268-65	1.8	0.2	1.2	0.2	0.2	20
880-606	2.0	0.2	1.3	0.2	0.3	25
[1] Critical Level	1.5	0.1	0.5	0.1	0.1	12

[1] Critical levels taken from Will (1985).

Table 11.4

Effect of nitrogen fertiliser compounds at three orchard sites on the number of strobili per ramet and the number of strobili in the first annual cycle of growth. Data are presented as mean values per ramet.

Site	Fertiliser compound	[1]Strobili per ramet	[1]Strobili per whorl
Amberley	Control	11.53[a]	3.69[a]
	$CaNH_4NO_3$	5.33[b]	2.26[b]
	KNO_3	12.15[a]	3.52[a]
	Urea	4.85[b]	2.50[b]
	Calculated probability level (Pr>F)		
	Clone	0.0001	0.0001
	Fertiliser	0.0001	0.0001
	Clone×Fertiliser	0.3729	0.0207
Te Teko	Control	2.78[a]	5.71[a]
	$CaNH_4NO_3$	2.23[a]	4.85[a]
	KNO_3	1.81[a]	5.14[a]
	Urea	2.15[a]	4.42[a]
	Calculated probability level (Pr>F)		
	Clone	0.0001	0.0001
	Fertiliser	0.0659	0.7836
	Clone×Fertiliser	0.5792	0.8277
Matakana	Control	19.70[a]	n/a
	$CaNH_4NO_3$	17.60[a]	n/a
	KNO_3	21.02[a]	n/a
	Urea	21.50[a]	n/a
	[2]Calculated probability level (Pr>F)		
	Clone	0.0001	
	Fertiliser	0.6304	
	Clone×Fertiliser	0.7846	

[1] Values without a common letter differ at the 5% level as per a Fisher's protected LSD test.

[2] Significance testing was carried out on $\log_e$-transformed data.

D. DISCUSSION

This study set out to establish whether nitrogen fertiliser application around the time of seed-cone bud differentiation directly increased strobilus production. It was of interest to establish if part of the unexplained variance in counts of strobili across sites in Chapter 4 was likely to be due to variation in soil mineral levels, particularly those of nitrogen.

On the basis of global literature it was expected that if nitrogen played a role in the outcome of axillary bud differentiation that the very high rates of elemental-N applied during February in this study would increase the numbers of emergent strobili carried by ramets at anthesis, across a range of orchard sites.

Overall, on no site did any form of nitrogen significantly increase strobilus production, either within the first annual cycle of growth or in the whole crown.

The forms of nitrogen fertilisers applied covered the spectrum of ammonium, nitrate and a mixture thereof.

The results indicated a strong site × N-form fertiliser interaction, with the 2 ammonium forms heavily reducing strobilus production per ramet and per whorl at Amberley, but not at Matakana. It would be of interest to try and interpret this difference in terms of existing nutritional status of the 2 soils at each of the sites; and their pH. But these data are not available for the soil at the Matakana site.

The results confirm those reported by Sweet and Hong (1978) who also tested the application of both ammonium and nitrate forms of N-fertiliser through a period from the 29th of October to the 30th of March on strobilus production in radiata pine. On the basis of their work there does not appear to be any basis for applying N-fertilisers to "well-fed" seed orchards at the time of long-shoot primordia initiation, to increase the number of seed-cone buds that begin differentiating. The results of the present study have now extended the findings of Sweet and Hong (1978) on to a range of different soil types and environments; and there has been no change in the strobilus production responses to liberal applications of N-based fertilisers.

Clearly, providing that N levels of soil are adequate to support crown development, applications of N-fertiliser is unlikely to further enhance strobilus production.

Because strobilus counts were made 6 months after N fertiliser application, there was no opportunity to establish if the fertilisers increased crown growth such that more sites for strobilus initiation developed. Thus the study looked only at direct effects of N fertiliser on strobilus production. It is likely that N effects on strobilus production are associated with crown growth rather than seed-cone bud differentiation *per se,* and that in the longer term the fertiliser may increase the total number of strobili carried by the whole crown rather than the number of those within individual whorls (Smith, 1987).

Considering it is not possible to increase strobilus production in seed orchards by N fertiliser application there is not likely to be any special merit in selecting orchard sites that have soils high in nitrogen. In fact, based on the findings at Amberley, there may possibly be deleterious effects on strobilus production if sites with very high soil N are selected. The Amberley findings also do raise the question as to whether many of the coastal sites are high strobilus producing ones because, along with conducive temperature conditions, the soils are predominantly sands which are inherently low in nitrogen.

In essence there do not appear to be gains to be made by maintaining high soil nitrate-N levels in seed orchard soils; further there is no evidence that the inclusion of a soil nitrate-N variable in the strobilus production model (Chapter 4) would improve its predictability.

CHAPTER 12

SUMMARY AND GENERAL DISCUSSION

A. INTRODUCTION

The intent of the research reported in this thesis was to obtain information on the relative levels of production of female strobili of *Pinus radiata* in different parts of the South Island; and to relate this to climate and site. The basic rationale behind the study was to improve the capacity of managers to select productive seed orchard sites.

In the past, seed orchards in New Zealand were sited in a rather *ad-hoc* fashion. Logistical reasoning usually overrode the limited biological understanding (much of which was anecdotal in nature) on the impact of site conditions on seed orchard productivity. Based on the yields from Amberley seed orchard, and the fact that summer water stress was thought to play a key role in strobilus production, the eastern South Island was considered to be the optimal general area for seed orchard productivity.

Just prior to the beginning of this study the demand for control pollinated seed greatly increased (Vincent, 1993), and there was a realisation that New Zealand's seed orchard capacity required expansion. One of the key issues was where new orchards should be sited in order to capture maximum productivity. Following discussions with the New Zealand Seed Orchard Research Group it was agreed that the need existed to establish a greater understanding of radiata pine strobilus production in relation to site and climate in the broadest sense. It was proposed to undertake this task by measuring strobilus production across a range of sites and climates in the South Island, and then to develop mathematical relationships between site conditions and strobilus data. The understanding obtained should then have value for the judicious selection of seed orchard sites.

The study was not intended to further understanding of the physiology of strobilus production; rather the intent was to identify key environmental variables linked to strobilus production, that could be used in an empirical model to screen potential sites.

B. REITERATION OF THE MAJOR FINDINGS OF THE STUDY

The multiple regression model developed in Chapter 4 identified 4 parameters which contributed significantly to explaining the variability in strobilus production across the sites studied. They were as follows (with their percentage contribution in brackets):

(i) Mean minimum temperature for February (approximately the time of long shoot differentiation) (54%).

(ii) Soil water stress integral for February and March (approximately the time of long shoot differentiation) (6%).

(iii) Accumulated growing degree days for the spring prior to strobilus differentiation (4%).

(iv) Mean minimum temperature for May (between differentiation and anthesis) (1%).

2 of the 4 parameters related to the time of strobilus differentiation (explaining a total of 60% of the variability) and one to the period between differentiation and anthesis (1%). The last one related to vegetative growth of the crown in the period prior to long shoot initiation (explaining 4% of the variability). The high level of inter-correlation between all temperature parameters is well recognised; and there is also of course a level of inter-correlation between temperature and soil water stress. Finally, of course it is recognised some of these parameters may influence strobilus numbers only indirectly, by increasing vegetative growth.

In the experimental sections of the thesis, the importance of each of these parameters was confirmed. Some of the components were confirmed in a more satisfactory manner than others.

C. CONTRIBUTION TO THE LITERATURE

Perhaps the synthesis of the international literature with which this programme started was that flowering in woody angiosperms, and strobilus production in conifers, was associated with hot dry summers. The standard interpretation of this has been that those climatic factors contributing to high carbohydrate levels in the tree, associated with those causing water stress,

were the key factors in promoting flowering. Temperature *per se* has not been overlooked as a causal factor because increasing it through the use of artificial temperature houses has been a very significant tool in improving the "flowering" of trees from boreal areas with harsh climates. It is suspected, however, that temperature has been generally seen as a less important contributor to flowering in countries with temperate climates.

At the time when this research started, it had not been widely suggested in New Zealand that an increase in strobilus production would occur with warmer temperatures: in fact the siting of recent New Zealand seed orchards in the drier parts of the South Island reflected the clearly held view that soil water stress rather than temperature was the key factor associated with high strobilus production. Thus the finding in the model of the importance of temperature to strobilus production of radiata pine was to some degree unexpected.

Radiata pine is a temperate coastal species with a reported optimum day/night temperature for vegetative growth of 20/5°C (Hellmers and Rook, 1973). The meteorological stations with high mean minimum February temperatures associated with optimal strobilus production are largely coastal, and do not have the day/night temperature differential reported as optimal for the vegetative growth of radiata pine. An example would be Waitangi Forest in the Bay of Islands which has a mean February temperature of 19.9°C and mean minimum night temperature for February of 10.6°C (N.Z. Meteorological Service, 1983). Thus it seems apparent that the optimum temperature range for strobilus production may be different from that for vegetative growth.

The two (February and May) temperature components uncovered by the model in Chapter 4 were also somewhat at variance with the current perceptions when the research started. If temperature was important, the perception at the start was that this related to the time of strobilus initiation and/or differentiation. The perception we now have from Chapters 3 and 8 of the importance of winter temperature in reducing the loss of differentiated strobili, is a new one.

Thus on balance, perhaps what the model has done to the knowledge perceptions for radiata pine at the beginning of the study has been to down-play the importance of summer water stress, and modify the perception held regarding the importance of temperature. It is probably less the incidence of hot summer days that is important to the species reproduction, but rather

the presence of a warm insular climate, changing little from day to night or month to month.

If such an interpretation is correct, it almost certainly differentiates radiata pine from a number of the North American and European conifers which occupy extremely continental climates. It is difficult to believe that their reproductive behaviour, as well as their growth behaviour would not have adapted to those climates.

The above interpretation and the temperate evolutional history of radiata pine, also leads to questions as to what is the upper limit of mean February minimum temperature for strobilus production in radiata pine? The results of the polyethylene house treatment in Chapter 8 would appear to indicate that there are levels of absolute temperature which are inhibitory to strobilus production. Similarly, the findings of the glasshouse treatment in the same chapter would indicate that some levels of seasonal and/or diurnal cooling in winter are also necessary for optimal strobilus production.

Unfortunately the model does not answer the question of the upper limits of temperature. Because the model was initially developed as a South Island one, its extension to the North Island was quite limited, and it is very under-represented in the warmest parts of New Zealand. However, the sites which were sampled with the warmest mean February minimum temperatures had the highest numbers of strobili. Thus there appears no reason to believe that the relationship peaks in New Zealand. There is evidence, however, that it is becoming asymptotic.

D CONTRIBUTION TO KNOWLEDGE OF THE PHYSIOLOGY OF FLOWERING

As indicated earlier, this was not intended to be a physiological study, and thus any contribution to physiology would be ancillary to the main objective. Perhaps the major physiological contribution made by the study is the support it offered the pioneering observations of Silen (1973a) that differentiation of strobili is not a simple "one off" process. The experiment in Chapter 8 where strobili initiated and differentiated at Amberley seed orchard were moved to a range of other sites for the winter before being returned to Amberley for anthesis was clear cut in its findings. The results made it very clear that the number of strobili differentiated in February is not the number which appear at anthesis; and that the loss is climate dependent. Again, the South Island was somewhat unfortunate. With the benefit of hindsight it would have

been of interest to over-winter some grafts in the warmest parts of New Zealand. The glasshouse substitute that was used was not adequate.

In terms of future physiological research, another outcome of the research which was particularly successful was the technique used in Chapter 7 to ascertain the timing at which "flowering" treatments would be effective. The treatment of moving grafts to a very low light intensity environment for a critical 2 week period proved an excellent way to "switch off" strobilus production. As a technique it could probably be used in the seed orchard, with appropriate tree covers. The literature is quite limited in such techniques.

The final physiological issue which needs discussion is the implications of the research by Dickson, Riding and Sweet (1994).

Major knowledge of the seasonal timing of initiation and differentiation has come from work with 6-year-old grafts (Bollmann and Sweet, 1976) and 10 to 12 year old trees (this thesis). In both cases, February was found to be the time of differentiation of long shoots in the first cycle of annual growth.

The first study to look at this timing in younger grafts was that of Dickson, Riding and Sweet (1994). It was carried out towards the end of the thesis, and it was totally surprising to the authors to find a major effect of ramet age on the timing of initiation and differentiation (see Appendix A). Until that finding, it had been assumed in all experiments to influence strobilus production, that treatments were being applied at the time of long shoot differentiation.

Another implication of the Dickson, Riding and Sweet study relates to gibberellin applications in seed orchard management. If the study is borne out by subsequent work, it means that the optimal time for gibberellin application, as defined by Siregar (1994) is not (as previously thought) at the time of bud differentiation.

The Dickson, Riding and Sweet paper has created problems for the writing of this thesis. If its findings prove to be correct, the buds of the younger grafts treated in Chapters 7 and 8 were <u>not</u> at the same developmental stage in February as those in the forest trees from which the predictive model in Chapter 4 was developed. Thus it could be argued that the experiments were not in fact strictly testing the findings of the model.

Essentially, it is not possible to take this issue any further at the present time. The Dickson, Riding and Sweet paper reported indicative and opportunistic information only: it was based on limited sampling of one clone in one orchard in one year; and it may not stand up to repetition in a more formal manner.

If it can be substantiated in further work, then there are some interesting issues to consider. Mid to late-February for example has been shown to be the optimal time for $GA_{4/7}$ application to both 1,2 and 3-year-old grafts in the meadow orchard. And yet Dickson, Riding and Sweet (1994) suggested that the timing of bud development in February is very different in the 3-age classes. The implication of that would be that February is an important time to treat grafts *per se*; and not because it reflects a certain stage of bud development.

In writing this thesis the decision was taken that it was unhelpful to speculate on these issues until the Dickson, Riding and Sweet study had been repeated in a much more formal manner. Thus in discussing the effects of treatments in February, no specific comment will be made on the stage of bud development at that time, or its significance.

The first experiment reported in Chapter 7 confirmed clearly that, in 1-year-old grafts at Amberley, the key time to influence strobilus production environmentally was between mid-February and mid-March. Placing grafts in a "non-flowering" environment during that time (and that time only) completely prevented strobili being formed. That experiment alone set the timing for the application of subsequent experimental treatments.

E THE SURVEY, THE MODEL AND ITS VALIDATION

1. The Strobilus Model

Research by Bollmann and Sweet (1976) and Sweet (1979) indicated February as being the month when long shoots differentiated into either strobili or branches; and when treatments to increase numbers of strobili were effective. Thus the climatic variability across sites during that month was one of the early parameters explored. Sites for the study were restricted to the eastern side of the South Island on the assumption that such sites covered the full spectrum of variability in strobilus production for New Zealand. That assumption was of course subsequently shown to be incorrect.

When it was found that strobilus production was more related to temperature than water stress, it was decided that, considering site temperatures are higher in the North Island the study should be extended to include some North Island sites. That extension was done as part of the validation process.

In the 1994 validation, there was general close agreement between the observed and predicted values for the strobilus model across the South Island. However, when validation sites for the North Island were included there was less agreement in the values, with the model both over-predicting and under predicting at different parts of the temperature range. Considering that the model originally was not able to account for some 34% of the between-site variance, it was not unexpected to find a level of discrepancy between the predicted and observed values. Nonetheless it was considered appropriate to establish why the model was less able to predict strobilus counts at the lower and particularly the upper end of the temperature range.

The validation study clearly indicated that the linear model was least appropriate for predicting strobilus counts at the upper end of the temperature range. Accordingly the appropriateness of a non-linear model for the data was explored. Of the various climatically-related parameters in the model, only those collected routinely as meteorological data could be easily used to screen the country broadly for potential seed orchard sites. The 2 parameters meeting this requirement were the mean minimum temperatures for February and May; and of those the one most related to strobilus productivity across sites was the mean minimum temperature for February. Thus It was decided to fit a non-linear model to the strobilus data for the 74 sites using long term mean February data as the only variable. The issue at this point was the selection of an appropriate non-linear function that would satisfactorily fit the data, bearing in mind that the number of sites at the high temperature end of the range were limited.

A series of growth functions were fitted to the data, namely the Schumacher, Hossfields, the modified Gompertz; and a logistic equation (see Chapter 5). It was only the Schumacher function, however, that met the convergence criteria and gave parameters significantly different from 0. Compared to the Log_e-linear model the Schumacher tended to have less under prediction and over-prediction (as per residual plots). Nonetheless in biological terms it still did not satisfactorily model the strobilus data as there were insufficient data points at the high temperature end of the range to produce the classical S-shaped response curve that might be expected. It was considered, however, that this model fitting exercise clearly supported the

development of a non-linear strobilus production model.

2. Other Tree Parameters

It was realised that due to abortion of reproductive structures between anthesis and seed set, counts of emergent strobili were not necessarily an indicative measure of the realisable seed yield at a site. To establish whether other variables in the seed production equation were related to strobilus production patterns, data were collected for conelet abortion and cone seed yield and weight.

The level of conelet abortion was independent of the numbers of emergent strobili across sites. Thus, regardless of the number of strobili carried by trees in the spring, varying levels of conelet drop occurred during the summer. The fact that the mean abortion level over the 52 sites was nearly 40% has implications for seed orchard managers who are concerned at comparable levels in their orchards.

Seed weight was also unrelated to strobilus production, but seed number was correlated. The higher strobilus-producing sites tended to yield more full seeds per cone.

3. Prediction of Sites Countrywide

It was apparent from the maps generated to indicate mean minimum February temperature that the sites with the highest values are coastal, particularly occurring on headlands and capes. There was also a significant effect of latitude, with high temperature sites decreasing in southern regions.

There are a number of inland locations in New Zealand which have very high day-time temperatures in February, but do not carry heavy crops of strobili. It was noteworthy that those regions do not have high mean daily minimum temperatures in February; and this perhaps explains the selection of minimum temperature by the model rather than mean temperature. The selection of high minimum temperature is in fact a selection for places with oceanic as distinct from semi-continental climates.

F. THE EXPERIMENTAL WORK

Following the development and validation of the strobilus production model, a number of experiments were conducted to verify the significance of the environmental variables selected by the multiple regression analysis (Chapter 4).

1. Temperature

It was evident from the model that of all the environmental variables selected into the equation the mean minimum February temperature was the one that accounted for most of the between-site variance.

The first experiment considered the effect of air temperature during February on seed-cone bud differentiation. Potted grafts were warmed and cooled during part of January and the whole of February and March. The results indicated that across all clones fewer grafts carried strobili when they were cooled during this time. However, holding grafts in a polyethylene house where they were warmed, completely eliminated strobilus production and caused abnormal growth.

Considering it was possible to reduce strobilus production through graft cooling it was unexpected to find that it was not possible to promote it through graft warming. While the reasons for this are not fully clear, the presumption must be that the maximum temperatures inside the polyethylene house were too high for seed-cone bud differentiation to take place. In the hottest parts of New Zealand radiata pine has been found to carry strobili on sites where the mean maximum temperatures are around 23°C and in Hawaii where temperatures were recorded at around 18.7°C. Clearly these temperatures are lower than those that were recorded in the polyethylene house and no knowledge exists of *Pinus radiata* growing or producing strobili at sites with maximum temperature events above 30°C.

Despite not being able to promote strobilus production through warming of grafts the findings of this experiment did indicate that cooling during February and March suppresses strobilus production. This result is in strong agreement with the strobilus production model which implicates decreased strobilus production with cool site conditions during February and *vice versa*.

It was also found that temperature conditions some 4-5 months following the start of strobilus differentiation influenced the number of structures that maintained reproductive potential. With increasingly cold temperatures during the winter at inland sites on the Canterbury plain it was found that differentiating seed-cone buds tended to switch to either branches or latent buds. On the other hand consistently warm temperatures during the winter in a heated glasshouse failed to retain strobili, but instead caused all seed-cone buds to switch to non-reproductive structures.

This finding indicated that in *Pinus radiata* the long shoot bud components are readily convertible for a considerable period of time after initiation. Further, that although environmental conditions during the time of strobilus bud differentiation predominantly govern the number of seed-cone buds forming, conditions quite late on in the winter also affect the number of strobilus buds that reach anthesis. Conditions favouring strobili are not only required in February but well into the winter. This finding was of course only new for radiata pine. It had previously been demonstrated for Douglas fir (Silen, 1973a)

2. Soil Water Stress

While soil water stress was found to be implicated in strobilus production at the stand level, its impact was much lower than that of temperature. As a single component the soil water stress integral for February and March explained 9% of the variability in strobilus production across sites; and as a component of the model it contributed 6%. The comparable figures for February temperature were 55% and 54%

To demonstrate this experimentally, the approach of irrigating grafts was found to be easier at an orchard level than water-stressing them. In the pot trial reported in Chapter 9, irrigating grafts through January, February and March reduced the number of emergent strobili at anthesis by 45%.

3. Growth

Temperature and rainfall conditions during the spring prior to the pre-long shoot initiation phase were found to be correlated with strobilus number. The effect of these variables was reflected in vegetative growth and crown development. Under experimental conditions it was not

possible to demonstrate a direct impact of spring weather on strobilus number, but branch number was significantly affected. In the longer term it was considered that this may affect the development of strobilus formation sites within the crown.

4. Nitrogen

Although not part of the strobilus model, N fertiliser applications at the field-scale level did not enhance strobilus production. Essentially, the results of this experiment extended the prior findings of Sweet and Hong (1978) across a range of different soil types. It is considered unlikely that there are gains to be made in New Zealand seed orchards by applying N-based fertiliser around the time of seed-cone differentiation. And it is unlikely that soil N levels will account for a significant proportion of the between site variation in strobilus production.

G HOW WELL SITED ARE NEW ZEALAND'S EXISTING RADIATA PINE SEED ORCHARDS ?

There are clear indications from the research in this thesis that they are probably in sub-optimal locations. The 2 orchards with the highest mean minimum February temperatures in New Zealand have probable values for this parameter between 13.8 and 14.0°C; while potential orchard sites exist in areas with temperatures of 17°C and above (Appendix E). It must be reiterated, however, that sampling of sites in higher temperature areas in New Zealand was limited, and no evaluation was made on those sites of conelet abortion, seed yields per cone or seed weight. The general perception of tree breeders (pers. comm.) is **not** that the warmer parts of New Zealand have very high cone yields, and there is a clear need to follow up the study in that direction.

But irrespective of whether the far north of the country is prolific in its cone production, it seems strange that companies which have orchards in the Bay of Plenty with mean February minimum temperatures of around 14°C should be setting up their new orchards in areas where the comparable value is between 11°C and 13°C. Unfortunately there is no published data to compare the seed production of recent orchards across a range of sites. But on the grounds of the model, it would seem logical to establish all future orchards on warmer North Island sites, **unless** some counter reasons exist to favour the South Island.

The issue of managing a control pollinated orchard on sites which promote vigorous vegetative growth is one which has arisen in the past, and may be relevant to some warm sites. Many of the warmer sites in New Zealand however are associated with soils which have physical and/or nutritional limitations which would restrict growth. They would be worth exploring from a strobilus production perspective. Such a suggestion raises the issue of how new seed orchard sites should be located.

H. PERCEPTION OF AN OPTIMAL SITE FOR STROBILUS PRODUCTION

54% of the variability in strobilus production across sites was explainable in terms of mean minimum February temperature; and Figures 5.7 and 5.8 provides a broad breakdown of New Zealand by this parameter.

It is unfortunate that, because this outcome of the model was not anticipated, sites in the upper end of the temperature range were not adequately sampled. Counts of strobili were made at only 3 sites with a mean minimum temperature higher than 15°C and the model under-predicted for those sites. Nonetheless, they are clearly some of the highest sites sampled, in terms of strobilus production.

While further sampling of forests with mean minimum February temperatures greater than 15°C is clearly needed, the model must in the mean time point towards such sites for future seed orchards. Essentially they exist in coastal areas north of Auckland and on the Coromandel Peninsula.

Such sites almost by definition will also have high mean minimum temperatures for May and a high number of accumulated growing degree days from August to November. They will not necessarily, however, have high levels of integrated soil water stress for February and March.

In soil terms, many of the sites in these areas are heavy clays and sands. Unless volcanic in nature they are not generally of high fertility. As indicated in Chapter 4, there is no reason to look for high fertility soils.

An issue which has proved troublesome in the past, at Papamoa orchard near Tauranga with a mean minimum February temperature of around 14.0°C is excessive vegetative growth

leading to management difficulties in hedging the orchard. This could probably be reduced on soils of lower fertility, with lower rainfall; to the benefit of strobilus production. Irrespective of that, current management techniques are less affected by vigorous vegetative growth than were earlier ones.

I. THEORETICAL CALCULATIONS OF REALISABLE SEED YIELDS - BASED ON DATA GATHERED FOR THIS THESIS

The collection of strobilus and other data for the seed production equation allows calculations for realisable seed yield from the top 2 metres of crown to be made, in order to demonstrate the total impact site plays on this variable. It is not intended that the yield values calculated below should be taken as predictions of potential seed orchard productivity *per se*. Rather they are used as a means of demonstrating relative differences between sites. The calculations do not allow for clonal variability in seed yield. And further no allowance has been made for losses due to cultural practices in seed orchards (e.g., seed loss due to pollination bags), pests (e.g., opossums) or climatic catastrophes (e.g., wind storms).

Firstly for the most productive 10 sites in the 1992 survey study the mean level of survival of the 21.85 strobili was 62% and the average number of full seeds per cone was 127; with each seed having a mean weight of 0.0319g. It was calculated, based on those data, that the mean total seed yield from the 2 metre crown region was 54.8g compared to 21.0g for the mean of the 52 sites (based on 9.38 strobili, 62% strobilus survival, 113 fulls seeds per cone each with a mean weight of 0.032g). If the 2m crown was regarded as a 2m ramet, then at a site with mean environmental conditions of the most productive 10 sites it could be expected that ramets would yield some 2.5 times more seed than ramets at a site with mean conditions for the 52 sites. Some 92% of the difference in seed would arise from differences in the number of strobili at anthesis.

J. LOCATION OF NEW SEED ORCHARDS

It would seem logical to use temperature maps (Figures 5.7 and 5.8) as the first entry point to seed orchard selection. And that proposal raises the question as to the accuracy of the fine detail of the maps. A comparison of the mean minimum February temperature of some of the warmer of the 320 meteorological stations for which long-term data exist (Appendix E), with

values shown by the map, shows a very close but not perfect correlation. But it indicates clearly the value of the maps as a starting point.

It is suggested that as an initial step, the model should be further validated in a general way in areas with mean minimum February temperatures greater than 15°C. On the basis of the model, trees in these areas should carry more than 40 receptive strobili in the top 2 metres of crown. And 90% of the trees in a stand should be carrying receptive strobili.

The issues of abortion, seed yields per cone and seed size have been shown to very important. Material in the Discussion of Chapter 6 suggested that the following parameters should be the accepted minimum: abortion below 30%, more than 120 seeds per cone, and a 1000-seed weight exceeding 35g.

Selection of a specific site within a general area of high strobilus production will always have an element of question, as a site is likely to be farm land, not carrying trees whose coning can be evaluated. The question of soils in respect of their structure, fertility and drainage will almost certainly be an issue; and there is little direct guidance that can be given. The nature of cone crops on comparable soils nearby is likely to be a key indicator, but the correlation in Chapter 4 between soil class and strobilus number should not be forgotten. Strobilus counts were higher on the yellow brown earths and sands than on the yellow grey and brown grey earths, but there was no strong correlation between strobilus number and soil phosphate level, pH or texture. Nitrogen levels in excess of those needed for normal growth and health are not required either (Chapter 10).

Soil moisture is an issue, and a soil which has the physical capacity to become moderately water stressed in the summer would be desirable. Rainfall for the months of January, February and March in the areas north of Auckland varies moderately between 190 and 320mm. It may be easier to control soil moisture through selecting for soil type than for low rainfall.

Personal comment from knowledgable observers (D. Bartram; Prof. G.B. Sweet) suggests that the process of selection of sites north of Auckland may not be as straight forward as the above suggests. While overall, there are good examples of heavy strobilus production, there are also examples of places such as Aupouri forest which carry many fewer cones than the model would predict. The extreme complexity of the soils in the region, and their deficiencies in a number

of major and minor elements may be an issue.

The importance of May temperature should not be overlooked. There is more than 5°C difference in mean minimum May temperatures in meteorological stations north of Auckland (7.5°C to 12.8°C). As for mean minimum February temperatures, the places with high values are all very close to the sea, and there are strong arguments that new seed orchards should be coastal. In that context, the very high strobilus production of the most coastal examples of radiata pine in its natural environment in California (Prof. W.J. Libby; Prof. G.B. Sweet, pers. comm.) are of interest.

At least in some parts of the country, quite major microsite effects exist in strobilus production (Somerville and Sweet, 1978). These may (or may not) be less in warmer than in colder parts of the country, but it would be important to look for them as part of any preliminary evaluation of sites.

K. FUTURE RESEARCH DIRECTIONS

As indicated during the course of this study a database comprising information on female strobilus production, along with climatic and soil information across sites, has been compiled. Accordingly this database could now be used to glean knowledge on the effect of environmental factors on other seed production variables.

1. Conelet Abortion

The incidence of conelet abortion in the post-pollination period causes considerable losses in all orchards, and currently no real physical means exist of reducing it at any site (Sweet, 1973) There would be considerable interest in reducing it by careful selection of site.

It follows that with little expense and effort it would now be feasible to model conelet abortion across sites using either the 1992 data or that data along with some new data collected across some North Island sites. Such an exercise would immediately yield information that would be useful for the future design of research attempting to understand and minimise conelet drop. Firstly, the results of the model would indicate whether or not conelet abortion was dependent on site and environmental conditions. Secondly, it may indicate which environmental variables

are the causal agents in the abortion scenario. Considering the lack of progress made during the past 10 or so years on conelet drop at the experimental level, the above approach has to be regarded as a logical next step.

2. Seed Quantity and Quality

Once strobilus production and retention have been optimised, seed yield per cone and seed size become important. Again, with a small extra collection of data from North Island sites it would be possible to explore the climatic contribution to these.

3. Pollen Archive Location

The increasing number of controlled pollinations being carried out in New Zealand indicate a need to establish new male orchards specifically for supplying pollen.

Although the strobilus model developed in this study indicated potential areas for female strobilus production, it would be possible to follow a similar procedure and develop a comparable model for predicting sites suitable for male strobilus production. There are several reports in the literature that pollen production in some *Pinus* species is promoted by elevated temperatures, particularly around the time of initiation (see Chapter 2). It is probable that pollen production in *Pinus radiata* is also correlated with temperature. If so, then it would not be difficult to utilise the methodology used in the development of the female strobilus model to develop a simple male strobilus model. Probably one would correlate temperature data during the time male cones are initiating/differentiating in December (Prof. R. Riding, pers. comm.) with a measure of pollen production in the spring.

Considering the majority of the seed orchards in New Zealand are presently located in the South Island, the opportunity exists to model male strobilus production and establish whether elevated temperature around the time of bud differentiation greatly increases the number of emerging male cones at anthesis. If this were the case then it would open up the option to locate male orchards in the warmer regions of the country, which would be conducive to optimal quantities of pollen being produced. And a northern location may mean that pollens would begin shedding either slightly before or at the same time as females were becoming receptive in the south. Clearly, this would allow more controlled crosses to be made using fresh rather

than stored pollen, which should augur well for the production of higher numbers of full seeds.

There are reports of inducing pollen production in grafts by cultural means. This information is scarce for radiata pine; indeed it would be difficult to make gains in this area very quickly due to the lack of knowledge on what treatments are likely to promote pollen production in this species. Obviously the approach of developing a model would assist in this. Besides, cultural promotion of strobilus production should only be considered once it is known that everything else in the orchard is optimal for strobilus formation. Clearly site has such a significant impact on female strobilus production that there is little reason to assume anything different for male cone production. Thus it is critical to select the right site before attempting to induce pollen through other means. It is likely that new male orchards are going to be established in New Zealand before any more seed orchards. Hence the research findings in this thesis now offer seed orchard managers the opportunity to further develop the female strobilus model to assist with prudent location of new pollen archives.

4. Seed Production in Controlled Environments

As alluded to to some extent in the last section, the option exists to use artificial environments or a range of cultural treatments to induce strobilus production in radiata pine clones. One reason such facilities have not been established in New Zealand is the associated cost of producing seed this way. If seed orchards are to remain the major output system for the radiata pine breeding programme it is important that they continue to produce seed at a competitive cost relative to micropropogation or vegetative cutting technologies. Obviously large breeding halls would only increase the cost of the seed. Their potential is much higher in countries with climates more adverse than New Zealand's.

The findings of this study, along with some prior knowledge on the significant impact site has on strobilus production, further discount the need for New Zealand seed orchardists to consider the need for intensive seed production facilities. Clearly, the problem of "sluggish" strobilus production in seed orchards, and probably other seed production problems, may be largely over come through the prudent selection of sites for seed orchard establishment. There is little doubt that, providing the conditions at a site are conducive for strobilus production, there are likely to be few gains to be made by attempting to produce seed in an artificial environment. The attempt to increase strobili in Chapter 8 in the polyethylene house and the glass house

certainly make one aware of the dangers of such treatments.

The use of cultural treatments for strobilus production should not be entirely discounted, however; rather a caveat might be to ensure that the right site for strobilus production is selected first, before attempting to further augment productivity via cultural means.

6. Intensive Seed Orchards

One of the key problems with seed orchards to date being that of the clones which are "shy flowerers". Because selection has not been for strobilus production, this has become quite a serious problem, and is one of the reasons that optimising orchard siting is so important. The fact that 100% of trees carried strobili on the best sites surveyed, compared to fewer than 30% on the poorest sites would appear to have implications for the "shy flowering" clones.

If studies were made of individual clones with low strobilus production, it might then be possible to meet their requirements more specifically than could a generalised orchard site. The use of root restriction bags which can be moved from site to site during the year offers potential in this respect.

Root restriction bags are made from a geotextile material, which is porous. When made into a plant pot and filled with soil the secondary roots of the plant are separated from the surrounding area; however, small fibrous roots that can grow through the pores seek minerals and nutrients from the surrounding soil. The pots restrict vegetative growth of plants without affecting their normal fruiting and seeding behaviour (Prof. R.N. Rowe, pers. comm.).

Growing grafts in these bags would allow them to be relocated to sites with sets of environmental conditions suited to the various phases of the generative cycle. For example, at the beginning of the growing season grafts could be moved to a site where they make vegetative growth such that optimal numbers of long shoot buds are initiated. Then in the months of December, January and February (during initiation and differentiation) they could be moved to a site where high summer temperatures prevail. The pots could be left above the ground so that the growing media becomes moderately water stressed. Then in March grafts could either be left at the warm dry site or moved to one where there is seasonal cooling, but the winter is frost free.

L. CONCLUDING STATEMENT

Clearly, strobilus production plays a major role in determining the yield of the seed crop at a site. In this thesis there is substantial evidence that site conditions greatly impact on the size of the strobilus crop at the time of anthesis. Although there is an ever increasing number of cultural treatments being realised for the promotion of strobilus production, a prudent first step by any tree seed orchardist would be to optimise the location of his or her orchard. Conducive site conditions for strobilus production are a good start to producing the quantities of seed needed to meet the ever-increasing demands by foresters.

The statistical model developed in this study and the supporting data and experimental evidence has delivered to the New Zealand seed orchard managers a tested tool not only to assist with judicious seed orchard siting, but also to augment knowledge on the other variables involved in the production of high quality radiata pine seed.

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APPENDICES

Appendix A

Manuscript prepared by Dickson, Riding and Sweet on the the effect of ramet size on the timing of female strobilus initiation in a Pinus radiata seed orchard clone.

This appendix contains a manuscript by R.L. Dickson, R.T. Riding and G.B. Sweet "Ramet size affects the timing of female strobilus formation in a *Pinus radiata* seed orchard clone.

The manuscript has been referred to in the text of this thesis. It reports a study undertaken in 1993 at Amberley seed orchard with clone 268-109. In that clone, potential strobilus-bearing buds from ramets aged respectively 2, 3 and 4 years from planting were dissected and microscopically examined on the 19th of February and 31st of March.

The aspect of significance is that the seasonal development of the buds in the 3 age classes differed. While long shoot primordia were differentiating strobili in buds of the 4-year-old ramets on the 19th of February; the 3-year-old and 2-year-old ramets were seasonally less advanced. It took a further 40 days (to 31st March) for the 2-year-old ramets to differentiate recognisable strobili. The 3-year-old ramets were intermediate in their timing.

The timing of strobilus differentiation in the 4-year-old strobili was as reported in the literature, and as observed in the buds collected from forest stands in this thesis. But the seasonal delay in development of the buds in younger ramets has not previously been reported.

It requires reiteration that the study was carried out on one clone at one orchard in one year. Nevertheless, both clone, orchard and year were used in the experimental work reported in this thesis.

The significance of the study for this thesis lies in the fact that this thesis used 1-year-old ramets for its experimental work in 1993, and 2-year-old ramets in 1994.

There is no question that the period mid-February to mid-March was an effective time to apply treatments to influence strobilus number. That has been documented very clearly in Chapter 7, and in recent studies of gibberellin application (Siregar, 1994). What becomes evident, however, from the manuscript in this appendix, is that strobili in clone 109 were not being differentiated at that time in 2-year-old, and presumably not in 1-year-old grafts.

The findings in the Dickson, Riding and Sweet (1994) manuscript only became apparent at the end of 1993, a time close to the end of the experimental work for this thesis. It was thus not possible to take them further as part of the thesis research.

It is considered premature to speculate on the physiological significance of the findings until they have been confirmed on a broader scale. So for the purposes of this thesis, the decision has been taken to simply recognise without comment that the treatments applied experimentally to 1- and 2-year-old grafts in Chapters 7, 8 and 9 were probably **not** applied to ramets at the time when their buds were differentiating strobili.

RAMET SIZE AFFECTS THE TIMING OF FEMALE STROBILUS FORMATION IN A *PINUS RADIATA* SEED ORCHARD CLONE

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RUNNING HEAD - Ramet size affects time of cone formation in Pinus

Summary

There is substantial variation in the timing of lateral long shoot initiation in Pinus radiata associated with ramet size. Grafted meadow orchard ramets aged 2, 3 and 4 years from planting (with respective heights approximately 1, 2 and 4 m) were sampled on February 19 and March 31. On February 19, microscopic examination revealed that vegetative and female strobili primordia were differentiating on 4-year-old ramets, but 2-year-old ramets had not initiated any lateral long shoot primordia. The 3-year-old ramets had vegetative and undifferentiated long shoot primordia but no female strobili. On March 31, buds on the 2-year-old ramets contained lateral long shoot primordia in early stages of differentiation. At this time strobili primordia of the 2-year-old ramets were similar in size and state of bract formation to those of the 4-year-old ramets 6-weeks earlier.

Key Words: bud development, cone formation, gibberellin ($GA_{4/7}$), histology, meadow orchard, megasporangiate strobilus, Pinus radiata, seed orchard

Introduction

In Pinus radiata D. Don, shoot formation at the apical meristem proceeds through the production of bud scales and then cataphylls with axillary short shoots or needle fascicles. After several needle fascicles have differentiated, the pattern of development changes, and a series of lateral long shoots is initiated. The subsequent development of long shoots may be into either branches or female strobili; alternatively, development may be arrested, resulting in lateral latent buds (Bollman and Sweet 1976). The time interval between the initiation of a lateral long shoot primordium and its recognisable differentiation into a branch or a female strobilus is approximately six weeks. The process of "decision making" during that 6 weeks has been called determination (Romberger 1963). There is evidence that a changing environment, even quite late during that period, may affect the outcome of determination (Silen 1973).

Studies of the timing of lateral long shoot initiation have been restricted to a few sites only, in a few years. The evidence generally indicates, however, that much of the 6 week determination period occurs during the month of February for strobili in the first annual cycle of growth. Thus, in commercial seed orchards in New Zealand, hormonal treatment with gibberellin ($GA_{4/7}$) to stimulate female strobilus development is carried out between mid-February and mid-March to coincide with this period of determination. The

effectiveness of treatment varies with year and clone, reflecting differences in the timing of determination between years and clones. There is also evidence that the effectiveness of $GA_{4/7}$ stimulation of female strobilus development declines with age of the ramets (Siregar 1994). This study was carried out on a single clone in a comercial seed orchard. We investigated the influence of ramet size on the timing of lateral long shoot initiation and determination.

Materials and Methods

On February 19 and March 31, 1993, terminal bud material was collected from three separate blocks of seed orchard plantings made respectively in 1989, 1990 and 1991. All plantings were at Amberley in the South Island of New Zealand, and all material collected was from a single clone. Approximate heights of the ramets in the three age classes were 4 m, 2 m and 1 m respectively. At each collection date, buds were taken at random from 5 ramets of each age class. Material from one typical ramet per age class was photographed.

Following each collection, the buds were sliced longitudinally and fixed in FAA (40% formalin/acetic acid/95% ethanol/water, 1/1/14/1, vol/vol/vol/vol) under vacuum for 24 h. Where lateral long shoot buds were present, they were dissected out and processed separately. The buds were dehydrated in a tertiary-butyl alcohol series and embedded in paraffin wax. Sections were made with a rotary microtome at 10-12 μm and stained in safranin-fast green (Johansen 1940) or toluidine blue (Berlyn and Miksche 1976). Sections were examined under a compound microscope and primordia were classified, on the basis of shape and presence of lateral primordia, as reproductive, vegetative, or undifferentiated (Bollman 1983). In the spring following collection, the mean date of anthesis was recorded for each age class of ramet, and counts of receptive strobili, vegetative long shoots, and

latent buds were made on 20 ramets of each treatment in the three age classes.

Data were analyzed by analysis of variance and, where appropriate, subjected to the Duncan's multiple range test.

Results and Observations

Status of the Shoot at Harvest

Figures 1A and 1B illustrate a typical bud cluster from one ramet from each of the 1989, 1990, and 1991 planting dates. Clearly, seasonal extension growth at both February 19 and March 31 was greater in the older, larger ramets. While the 1989-planted ramet had extended 14 cm above its basal branch cluster on February 19, the 1991-planted ramet only reached that length on March 31.

Apical Development

Bollmann (1983) found that, compared with vegetative buds, seed cone (strobilus) buds developed more slowly, but they had an apical dome which was larger, both in height and diameter. These differences in bud size were evident in the material studied (Table 1, Figures 2 and 3).

There were significant differences in developmental stage between buds of different-aged ramets (Table 1, Figures 2A-F). On February 19 differentiating strobili (height(h) = 588 ± 47 μm; diameter(d) = 730 ± 59 μm) were present in buds of the 1989-planted ramets (Figure 2C); vegetative buds were present

on 1989- and 1990-planted ramets (Figures 2B and 2E); and the 1991-planted ramets had no lateral long shoots (Figure 2F). Primordia continued to develop on ramets of all ages between the two sample dates. By March 31, buds from all planting ages had differentiating strobili, but there was considerable difference in their size and stage of development (Figures 3C, 3D and 3E). Strobilus buds on 1989 ramets [h = 1645 ± 62 μm; d = 1294 ± 69 μm] had increased significantly in size from February 19 (Table 1) and bracts were evident and expanding along the flanks of the primordia (Figure 3E). Strobilus buds on the 1991 ramets (h = 558 ± 36 μm; d = 753 ± 38 μm) were similar to those of the 1989 ramets on February 19 with little evidence of bract initiation (Compare Figures 2C and 3C). Strobilus buds on the 1991 ramets (h = 776 ± 69 μm; d = 894 ± 135 μm) were intermediate in size and bract initiation (Figure 3D). In addition, in the 1991 ramets development of vegetative buds had not proceeded as rapidly as development of reproductive buds. Although the reproductive buds were similar to those on the 1989 ramets on February 19, the vegetative buds showed no evidence of axillary meristems (Compare Figures 2B and 3B) and there were many undifferentiated primordia (Table 1, Figures 2A and 3A).

The pattern of bud formation was the same for all three age classes; the first-initiated lateral long shoots were usually reproductive, with the later-initiated ones being vegetative.

Status After Shoot Expansion

The dates of anthesis and nature of the first cycle lateral long shoots for the 1989, 1990, and 1991 ramets in the spring of 1993 are summarized in Table 2. Anthesis for the 1991-ramets occurred 4 weeks after the 1989-ramets. The 1991-ramets also had more latent buds than the older ramets ($p < 0.001$).

Discussion

Ramet size influenced the timing of initiation and differentiation of primordia. Larger ramets displayed earlier initiation and differentiation of lateral long shoots. Thus, by February 19 lateral long shoot primordia were already present and differentiating on the 1989 ramets. The long shoot primordia were at a stage similar to those reported for older conventional seed orchard trees on 27 February 1979 (Bollmann 1983). On the 1990 ramets initiation had taken place and differentiation of vegetative buds was evident (Figure 2E) while a number of the first initiated lateral long shoots were undifferentiated (Figure 2D). These primordia were similar in appearance to those reported by Bollmann (1983) for older trees on 24 January. This would indicate that developmentally the 1990 ramets were approximately 4 weeks behind the 1989 ramets on February 19. Long shoot primordia were not evident on the 1991 ramets (Figure 2F). Ramet size did not alter the pattern of differentiation of long shoot

primordia which was the same as that reported by previous workers for Pinus radiata (Bollmann and Sweet 1976, Bollmann 1983, Ross et al. 1984). The delay in initiation and differentiation of strobili primordia was carried over to the timing of anthesis. Thus, differentiation of strobili primordia in the 1991 ramets was 6 weeks behind the 1989 ramets and anthesis was delayed about 4 weeks.

The rate of differentiation of vegetative shoots on the 1991 ramets was slower than for the 1989 ramets. Delayed development of vegetative buds has been reported for cultural treatments which stimulate cone production (Ross et al. 1984, Owens et al. 1992). This might indicate that the younger material would be more susceptable to the enhancing effects of $GA_{4/7}$ than older material. Alternatively, the different rates of primordium development between the 1989 and 1991 ramets might reflect environmental conditions at the time of initiation, with earlier initiation occurring when conditions favoured vegetative growth and later initiation coinciding with conditions which would favour reproductive development. In other pines development of reproductive primordia continues later in the fall than vegetative bud development (Greenwood 1981).

Acknowledgement

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Table 1. Size (μm) of long shoot primordia above the last-formed cataphylls.

Year of Planting	Sample Date	Strobilus		Vegetative		Undifferentiated	
		Height	Diameter	Height	Diameter	Height	Diameter
1989	19 February	588[b]	730[b](8)[1]	212	400(17)	282	565(2)
	31 March	1645[a]	1294[a](6)	212	518(7)	-[2]	-
1990	19 February	-	-	188	447(6)	235	400(4)
	31 March	776[b]	894[b](5)	141	376(4)	165	306(1)
1991	19 Feburary	-	-	-	-	-	-
	31 March	558[b]	753[b](5)	165	329(7)	305	447(8)

[ab] - Within columns, means followed by different letters are significantly different (P = 0.01, Duncan's multiple range test)

[1]( ) - number of primordia measured

[2] - - no primordia in classification

Table 2. Date of anthesis and effect of ramet age on the number of vegetative branches, latent buds, and strobili borne laterally in the first potential cone bearing cycle of 1993.

Year of planting	Date of anthesis	Bud type	Average Number	SEM[1]
1989	22 July	Branch	1.5	0.56
		Latent	0.25	0.18
		Strobilus	5.0	0.40
		Total	6.7	
1990	27 July	Branch	1.1	0.44
		Latent	0.41	0.19
		Strobilus	5.7	0.35
		Total	7.2	
1991	15 August	Branch	1.5	0.40
		Latent	1.4	0.34
		Strobilus	2.6	0.95
		Total	5.5	

[1]Standard error of the mean.

Figure 1 Photographs of long shoot terminal bud clusters of representative ramets from each age class. A 19 February and B 31 March 1993. Bar = 5 cm.

Figure 2 Buds from ramets collected on 19 February. A - E Lateral buds from terminal buds. A - C Primordia from 1989 ramet (x60): A Undifferentiated, B Vegetative, C Reproductive. D and E Primordia from 1990 ramet (x60):D Undifferentiated, E Vegetative. F Bud from 1991 ramet (x6.5). a - Lateral bud.

Figure 3 Lateral buds from terminal buds of ramets collected on 31 March. A - C Primordia from 1991 ramet (x60): A Undifferentiated, B Vegetative, C Reproductive. D Reproductive primordia from 1990 ramet (x60). E Reproductive primordia from 1989 ramet (x35).

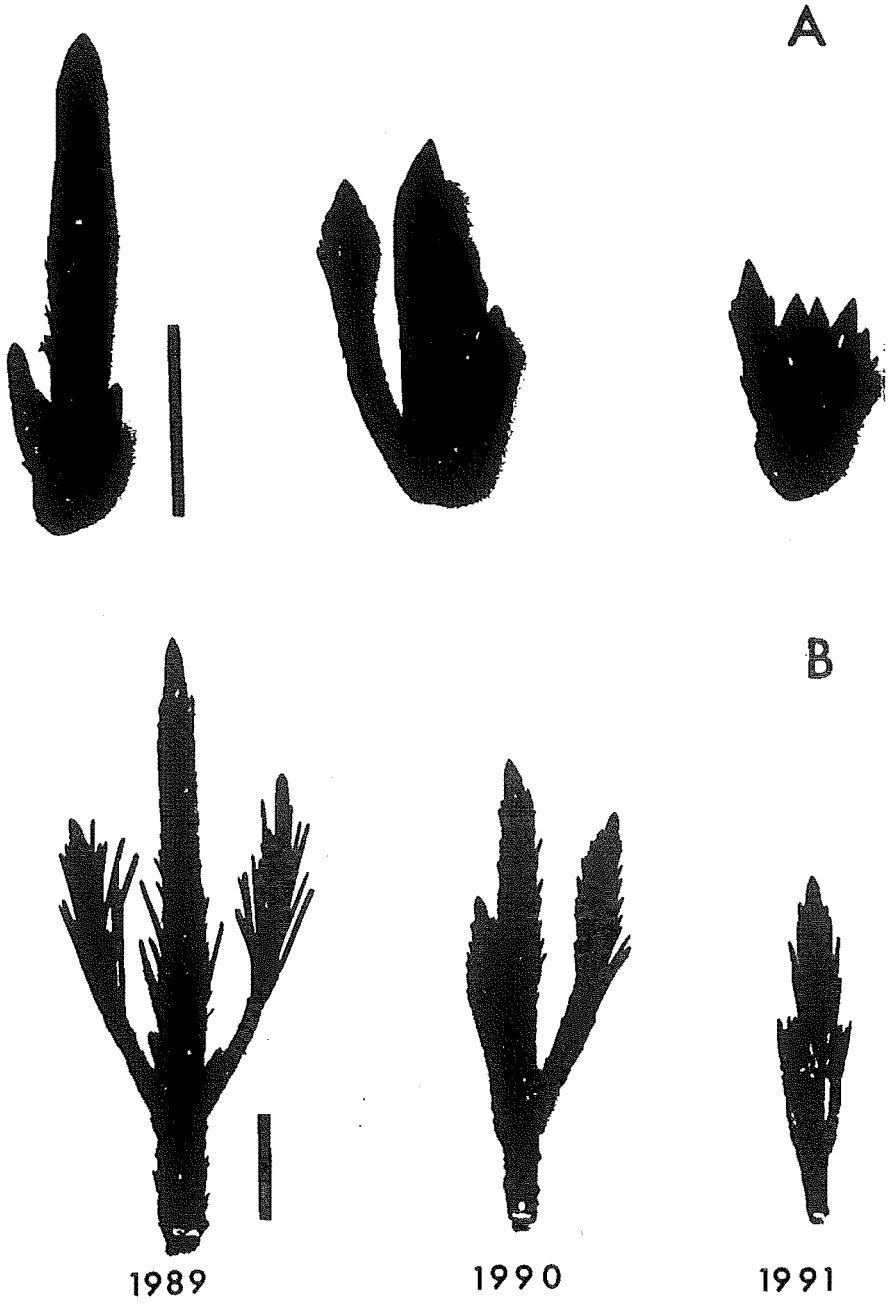

Figure 1 - Ramet size affects cone formation

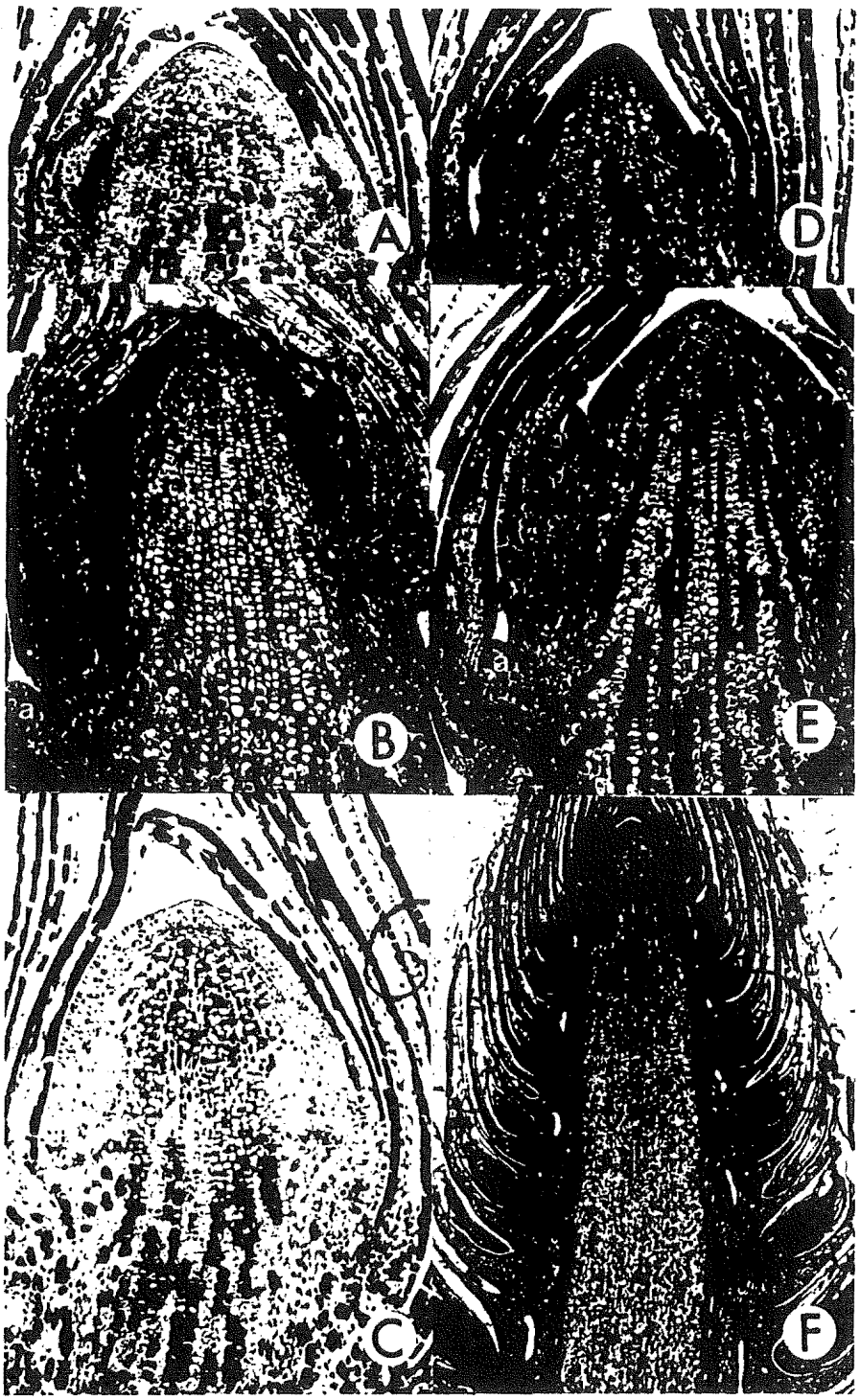

Figure 2 Ramet size affects cone formation

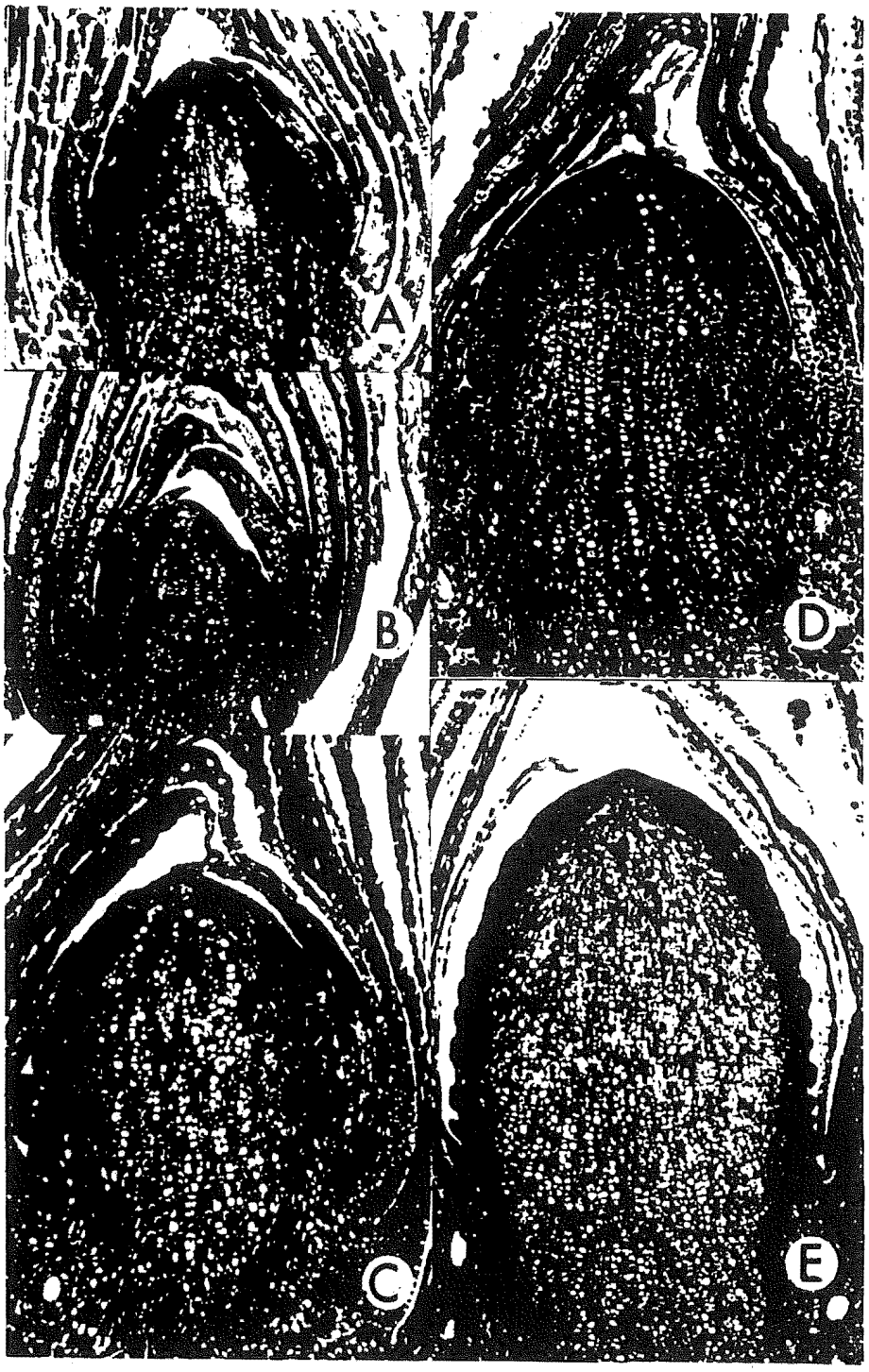

Figure 3 Ramet size affects cone formation

APPENDIX B

A description of a simple daily forest water balance model

This appendix comprises a document compiled by Dr. David Whitehead, of Landcare Research Ltd, which contains information on a simple forest water balance model. This information was used to write a water balance model in a spreadsheet which was then used to calculate soil water status for sites used in the survey studies; as well as for Amberley seed orchard. The spreadsheet used was Quattro Pro Version 5.0 for DOS. The spreadsheet was set to manual calculation and the row-wise recalculation option was also selected. Along with the model code the appropriate climate data for each site was imported into a notebook section of the spreadsheet. A separate spreadsheet file was made up for each site.

The model that was written was a simple tipping bucket one in the sense that the drainage function was set such that water was only drained from the soil once the soil water content reached field capacity.

A SIMPLE DAILY FOREST WATER BALANCE MODEL

Compiled by David Whitehead
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The water balance for a forest site will depend on weather, soil and vegetation properties. While these properties are known to differ between sites, the water availability at one site also varies from year to year because of differences in the amount and distribution of rainfall and solar irradiance. Weather conditions vary widely in time and space but the data required to run models is limited by the network of recording stations available and the frequency of measurement. The simple water balance model described below is a compromise between the detail required to estimate components of water balance with varying weather conditions, and the availability of weather data to run such models.

A daily resolution is used with a minimum weather data requirement of daily minimum and maximum temperature, rainfall and solar radiation. An section that allows estimates of solar radiation to be calculated where temperature data alone are available could be incorporated. Physical and drainage properties for the soil at the site, root zone depth and a value for root zone water content at the start of the modelling period are also required.

All of the functions included in this model have been widely used and tested elsewhere for forest and other crops. The equations are physically based and widely applicable. This is a compilation of work undertaken elsewhere to derive these models. References to the original sources can be found throughout the text.

Water balance

The canopy consists of trees and understorey vegetation and this is treated as a single layer. At present, no partitioning between layers or structure of vegetation is incorporated. Similarly, the root zone is treated as a single layer with uniform properties throughout the profile. The water balance can be described by the equation

$$S_j = S_{j-1} + P - E - F \qquad (1)$$

where S_j and S_{j-1} are the root zone water storage on day j and the previous day, P and F are rainfall, and drainage during the daily period. Evaporation, E, comprises transpiration from the dry tree and understorey canopies, E_t, and evaporation from the wet canopies during and after rainfall. All units are in mm day^{-1}. It is assumed that daily rainfall is available as an input variable.

Evaporation

Transpiration from the dry canopy

The model of evaporation is based on work by Black and Spittlehouse (1981), Spittlehouse and Black (1981), Giles, Black and Spittlehouse (1984), Spittlehouse (1985), Spittlehouse (1989).

Following Priestly and Taylor (1962) for dry canopy conditions the maximum rate of evaporation from the site, E_{max}, is energy limited and is a constant fraction of the equilibrium evaporation rate, E_{eq}, as

$$E_{max} = \alpha\ E_{eq} \tag{2}$$

where α is a coefficient and

$$E_{eq} = \frac{s}{\lambda(s + \gamma)} R_n\ . \tag{3}$$

R_n is the daily (24-hour) net radiation flux density (MJ m^{-2} day^{-1}) at the site. On a daily basis it is assumed that the components of soil heat flux density and energy storage in the canopy are negligible. The physical coefficient s (kPa $°C^{-1}$) is the slope of the saturation vapour pressure curve with temperature and γ (kPa $°C^{-1}$) and λ (MJ kg^{-1}) are the psychrometric constant and the latent heat of vaporisation of water, respectively, both weakly dependent on temperature (see physical coefficients). The empirical coefficient α is dimensionless and, for forest an appropriate value is 0.7 (Shuttleworth and Calder 1979, Spittlehouse 1989). Based on measurements made for a mature *Nothofagus* forest, Tate *et al* (1993) suggested a value for α of 0.6. Measurements of net radiation are rarely available from weather station data, but these can be estimated from measurements of solar irradiance (see below). If the units as shown are used then values for evaporation will be calculated in mm day^{-1} (noting that the density of water is 1000 kg m^{-3}).

In conditions of water deficit, the actual rate of transpiration, E_t, will not reach E_{max}, but will depend on the root zone water availability. The use of root zone matric potential, ψ (MPa, see below), rather than root zone water content, to determine the fraction E_t / E_{max} allows the model to be used at sites with different soil water retention characteristics. Following Whitehead and Kelliher (1991) evaporation is decreased by a coefficient ϕ (1 → 0) when ψ falls below a threshold value. E_t is equal to E_{max} and ϕ=1 until ψ reaches -0.02 MPa ("field capacity"). As ψ decreases below -0.02 MPa, ϕ is assumed to decrease linearly to 0 at ψ=-1.5 MPa ("permanent wilting point"). Thus

$$E_t = E_{max}\ \phi \tag{4}$$

and
$\phi = 1$ when ($\psi \geq$ -0.02 MPa)
$\phi = 1 + ((\psi + 0.02) / 1.48)$ when (-1.5 MPa < ψ < -0.02 MPa)
$\phi = 0$ when ($\psi \leq$ -1.5 MPa).

Evaporation from the dry and partially wet canopy

On days when the canopy is wet, a fraction of the rain falling is intercepted and evaporated. Since the presence of intercepted water decreases transpiration. However, during and after shortly rainfall the evaporation rate may be greater than R_n due to advective enhancement. Following Gash (1978), Shuttleworth and Calder (1979) and Spittlehouse and Black (1981), Giles, Black and Spittlehouse (1984) on days when rain occurs total evaporation, including both transpiration and evaporation from wet foliage is expressed as

$$E = E_t + gI \tag{5}$$

where I is the daily rainfall interception (mm day^{-1}) and g is a coefficient. From a range of studies of interception of rainfall by forest canopies it may be assumed that $I = 0.25\ P$ (mm day^{-1}), although this function could depend on canopy leaf area index. The value for g can be determined experimentally from analysis of rainfall and evaporation data (= 1 - $E_t / (\alpha_w\ E_{eq})$) where E_t is the rate of transpiration for the day if the foliage were dry and α_w is an empirical coefficient (usually between 3 and 5) relating evaporation from a completely wet canopy to E_{eq}. However, an appropriate value for g for forest is 0.8 although it has been shown to vary with root zone water content (Giles, Black and Spittlehouse 1984).

For simplicity, it is assumed that all intercepted rainfall is evaporated on the day when rainfall occurs.

Calculation of net radiation from measurements of solar radiation

Measurements of net radiation flux density, R_n for use in Equation 3 are rarely available, but these can be calculated from measurements of incident solar radiation flux density, K.

Daily average air temperature, T (°C), is calculated from measurements of daily minimum, T_{min}, and maximum, T_{max}, air temperature as $(T_{max} + T_{min})/2$. Net radiation flux density (MJ m^{-2} day^{-1}) is

$$R_n = (1-a)K + L \tag{6}$$

where a is a canopy reflection coefficient and L is the daily net longwave radiation flux density as

$$L = (c + d\ K/K_{max})\ (e_a - e_v)\ \sigma(T+273)^4 \tag{7}$$

(Spittlehouse and Black 1981) where K_{max} is the maximum possible incident solar radiation flux density for the day, ε_a is the apparent emissivity of the atmosphere, ε_v is the emissivity of the vegetation, c and d are constants and σ is the Stefan-Boltzman constant. An appropriate value for a is 0.12 and for ε_v is 0.96 (Jarvis, James and Landsberg 1976). ε_a is calculated from the Idso-Jackson formula (Aase and Idso 1979) as $\varepsilon_a = 1 - (0.261 \exp(-7.77 \cdot 10^{-4}\ T^2))$. Appropriate values for c and d are 0.1 and 0.9, respectively (Spittlehouse and Black 1981).

Daily values for K_{max} appropriate for the site can be calculated using solar geometry equations following Hungerford *et al* (1981). However, a simpler approach is to estimate K_{max} for different times of year from measurements of K made at or near to a site, then calculate it for each day using sine function of the form K_{max} (MJ m^{-2} day^{-1}) = $p + q \sin(0.0172 (J-81))$ where J is the day in the year (starting on 1 July for the southern hemisphere) and p and q are parameters.

Drainage

The root zone is considered to be a single layer with uniform physical characteristics and uniform distribution of root water uptake. In a freely draining soil, the drainage rate, F, is determined by the hydraulic conductivity (Gardner 1983) which can be expressed as a function of average root zone volumetric water content, Θ (m^3 m^{-3}, = S/ξ where S is the root zone water storage and ξ is the root zone depth, m) where

$$F = F_r (\Theta/\Theta_r)^f. \quad (8)$$

F_r is the drainage rate at a reference root zone water content Θ_r and f is a dimensionless coefficient that can be determined experimentally for individual soils. For the deep loamy sand in the pumiceous soil at Whakarewarewa Forest, Rotorua, values for the parameters F_r, Θ_r and f were 1066 mm day^{-1}, 0.533 m^3 m^{-3} and 30, respectively (Whitehead and Kelliher 1991).

An alternative, simple approach is to assume that drainage is zero until the root zone volumetric water content reaches field capacity, Θ_f (see below). Drainage is zero until Θ_f is reached, but when $\Theta > \Theta_f$, all further additions of water become drainage.

Root zone matric potential

Average root zone matric potential, ψ (MPa), is related to Θ by the soil water retention function

$$\psi = \psi_r (\Theta/\Theta'_r)^w \quad (9)$$

where ψ_r and Θ'_r are reference values and w is a parameter that can be obtained experimentally from measurements made in the laboratory on undisturbed soil cores following Campbell (1974). w can be calculated if measurements of ψ are known at two values of Θ. Often, measurements of Θ_f when the soil is at "field capacity" (ψ = -0.02 MPa) and Θ_w when the soil is at "permanent wilting point" (ψ = -1.5 MPa). A table of representative values for these parameters for a wide range of soil types is provided by Clapp and Hornberger (1978). For the deep loamy sand in the pumiceous soil at Whakarewarewa Forest, Rotorua, values for the parameters ψ_r, Θ'_r and w were -5 x 10^{-3} MPa, 0.46 m^3 m^{-3} and -4.82, respectively (Whitehead and Kelliher 1991).

Physical coefficients required for the model

The physical coefficients used in the model are dependent on the value for daily air temperature, *T*, as follows (written in software code for convenience)

s slope of the saturation vapour pressure curve with temperature (kPa $°C^{-1}$)
s1 = 0.61078*exp((17.269*(T+0.5))/(237.0+(T+0.5)))
s2 = 0.61078*exp((17.269*(T-0.5))/(237.0+(T-0.5)))
s = s1-s2

γ psychrometric constant (kPa $°C^{-1}$)
γ = (0.646+0.0006*T)/10.0

λ latent heat of vaporisation of water (MJ kg^{-1})
λ = (2.501-(0.0024*T))

σ Stephan-Boltzmann constant (MJ m^{-2} day^{-1} $°K^{-4}$)
$\sigma = 4.9*10^{-9}$

Operation of the model

The input weather variables needed for the model are:

daily values of solar radiation	K	MJ m^{-2} day^{-1}	Equation 6, 7
daily rainfall	P	mm day^{-1}	Equation 1
daily minimum air temperature	T_{min}	°C	Equation 6
daily maximum air temperature	T_{max}	°C	Equation 6

The site variables needed for the model are:

starting root zone water content	Θ	m3 m^{-3}	Equation 1
root zone depth	ξ	m	Equation 8, 9

The parameters needed for the model are:

parameters for estimating K_{max}	p, q		Equation 7
parameters for root zone drainage	F_r	mm day^{-1}	Equation 8
	Θ_r	m^3 m^{-3}	Equation 8
	f		Equation 8
parameters for water retention curve	ψ_r	MPa	Equation 9
	Θ'_r	m^3 m^{-3}	Equation 9
	w		Equation 9
or			
root zone water content at			
field capacity (ψ = -0.02 MPa)	Θ_f	m^3 m^{-3}	Equation 8
permanent wilting point (ψ = -1.5 Pa)	Θ_w	m^3 m^{-3}	Equation 9

For each day the components in Equation 1 should be calculated from weather data (rainfall, maximum and minimum air temperature and solar radiation) and the functions described above as follows.

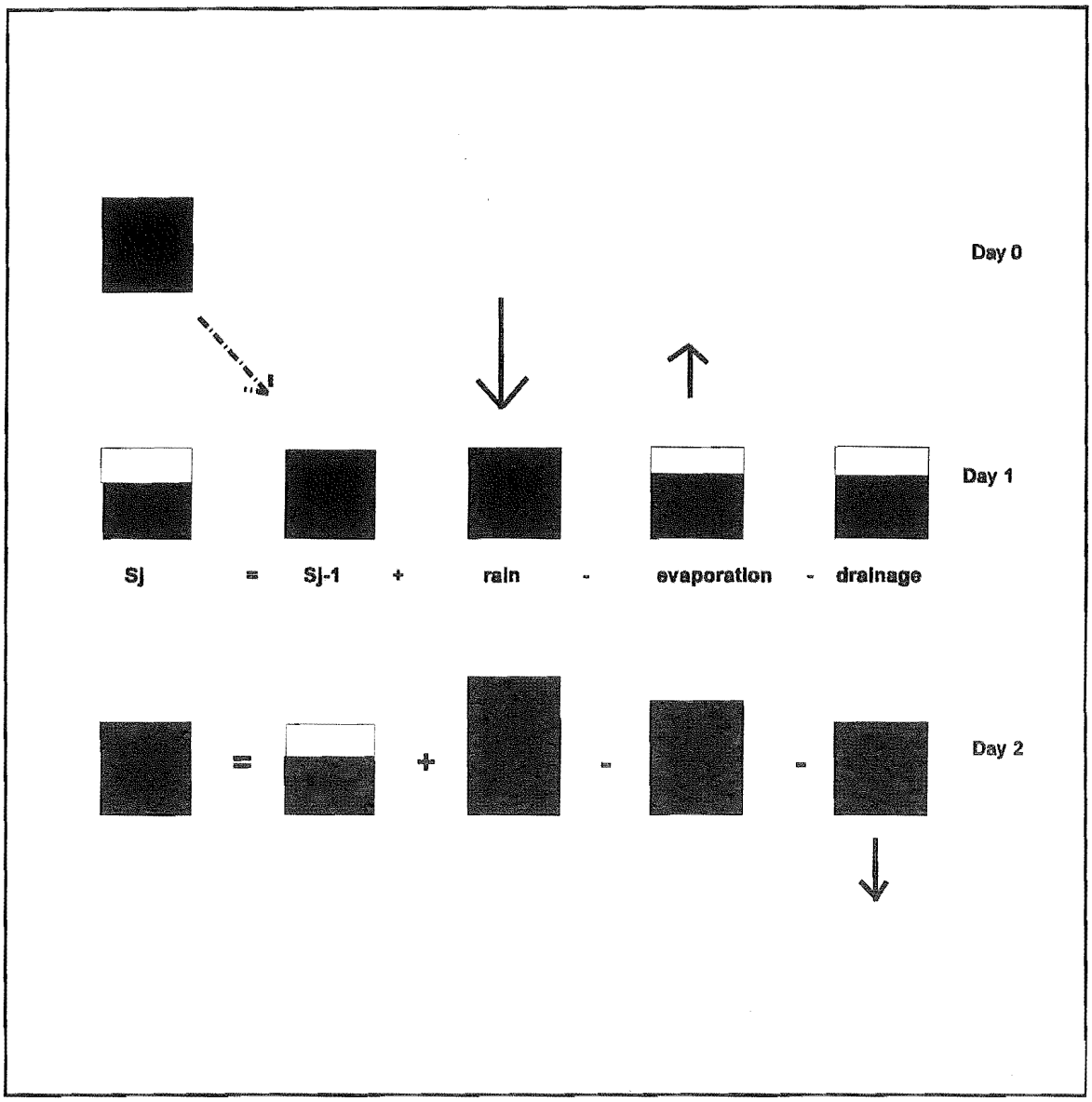
1. An initial value for S and thus Θ (= S/ξ) is required. Often the best time to start is in the winter months after a period of several days of rain, when it can be assumed that the root zone water content is at field capacity.
2. Input T_{min} and T_{max} and calculate T.
3. Input K and K_{max} to calculate R_n from Equations 7 and 6.
4. Calculate E_{eq} and E_{max} from Equations 3 and 2. Note that evaporation must not be less than zero.
5. Calculate ψ from Equation 9, then the value for ϕ and E_t from Equation 4.
6. Input P and calculate E from Equation 5.
7. Add P to S and subtract E from S in Equation 1 to give a new temporary S.
8. Calculate F from Equation 8, or

8a. For the simple model, when the new temporary S is greater than $\Theta_f\xi$ calculate F as $(S - \Theta_f\xi)$ where Θ_f is the root zone water content at field capacity. Note that if S is less than or equal to $\Theta_f\xi$ then F=0.

9. Subtract F from the temporary S to give the new S for the day.
10. Return to step 2 for the next day, keeping a running balance for S and totals for P, E and F.

A Schematic Diagram of the

Simple Tipping Bucket Soil Water Balance Model



The diagram illustrates the various components of the model: and the estimation of soil water content over a 2-day period.

In this diagram drainage is shown to only occur once the soil reaches field capacity. The drainage function in the soil water balance model written for the study was set up such that water was only drained from the soil once it reached field capacity.

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APPENDIX C

Predicted and actual soil water potential of the root zone of sites across the South and North Island during February 1994. The predicted values were obtained by using a tipping bucket soil water balance model set at 0.4m rooting depth.

Site	Date (1994)	[1] Plant AWC (%)	Root zone water potential (MPa)	
			[2]Predicted	Actual
Whangarei	7 Feb	0.37	-1.10	-1.30
Woodhill	7 Feb	0.03	-1.50	-1.50
Matakana Is	8 Feb	0.17	-1.50	-1.50
Murapara	8 Feb	0.11	-1.50	-1.50
Mohaka	9 Feb	0.50	-0.07	-0.07
Wairoa	9 Feb	0.48	-1.20	-1.50
Havelock Nth	10 Feb	0.29	-1.50	-1.50
Dannevirke	10 Feb	0.37	-1.50	-1.50
Martinborough	11 Feb	0.46	-1.50	-1.50
Levin	12 Feb	0.52	-1.50	-1.50
Cape Campbell	13 Feb	0.27	-1.50	-1.50
Grassmere	13 Feb	0.41	-1.50	-1.50
Rabbit Island	14 Feb	0.13	-1.50	-0.60
Hanmer	14 Feb	0.41	-0.90	-0.20
Peel Forest	19 Feb	0.25	-0.50	-0.50
Naseby	18 Feb	0.16	-1.50	-1.50
Dunedin	17 Feb	0.44	-1.50	-1.50
Balcultha	17 Feb	0.33	-1.50	-1.50
Kirwee	22 Feb	0.23	-0.04	-0.27

[1] Plant available water content - calculated by measuring the difference in gravimetric water content between field capacity and wilting point.

[2] Total daily water stress (intergral) for both February and March 1992 (as calculated by soil water balance model - Appendix B)

APPENDIX D

Description of soil texture across sites sampled in 1992

No	Site - 1992 sample	Mean No strobili (1992)	Soil Texture	[1] Plant available water content (%)	[2] Soil water stress Feb.-March (1992)
1	Rabbit Island	31.9	coarse gravel	0.13	-66
2	Motueka	28.4	silt loam	0.43	-86
3	Appleby	24.2	sandy loam	0.45	-84
4	Grassmere	20.1	silt loam	0.3	-52
5	Kaikoura	19.8	stoney gravel	0.15	-68
6	Northbank	19.6	silt loam	0.29	-65
7	Mcleans Is.	19.6	stoney sand	0.14	-69
8	Makikihi	19.3	silt loam	0.42	-72
9	Mayfield	18.5	silt loam	0.33	-62
10	Birch Hill	16.9	stoney loam	0.38	-42
11	Ashley For.	16.1	silt loam	0.3	-70
12	Blenheim	15.0	sandy loam	0.48	-60
13	Woodend	14.7	sand	0.05	-66
14	Moeraki	14.0	clay loam	0.63	-71
15	Waimate 1	12.6	loamy sand	0.38	-75
16	Salt Water Cr.	12.4	sand	0.01	-66
17	Awatere Vly.	11.5	silt loam	0.44	-50
18	Rakaia	11.5	silt loam	0.07	-74
19	Spotswood	10.3	silt loam	0.41	-40
20	Wairau Vly.	10.0	stoney loam	0.54	-33
21	Oamaru	10.0	silt loam	0.58	-70
22	Rangitata	10.0	silt loam	0.21	-71
23	Waimate 2	9.5	loamy sand	0.38	-75
24	Rainbow	9.3	stoney loam	0.43	-60

25	Winchmore	9.0	silt loam	0.21	-69
26	Lincoln	8.3	silt loam	0.07	-70
27	Rangiora Nur.	7.9	silt/sandy loam	0.46	-59
28	Kurow	6.5	stoney/sandy loam	0.44	-71
29	Spencerville	6.4	sand	0.05	-71
30	Lake Waihola	5.9	sandy loam	0.43	-16
31	Merivale Station	5.4	sandy loam	0.63	-62
32	Amberley B.	5.1	stoney gravel	0.03	-78
33	Orari	5.1	stoney/sandy loam	0.05	-81
34	Homebush	5.0	stoney silt loam	0.25	-60
35	Amberley	4.8	silt loam	0.32	-52
36	Tapanui	4.7	silt loam	0.37	-44
37	Darfield	4.6	silt loam	0.31	-44
38	Cromwell	4.5	sandy loam	0.17	-57
39	Balmoral	4.1	sandy loam	0.33	-43
40	Eyrewell-Wrights	3.9	stoney/silt loam	0.26	-60
41	Burkes Pass	3.8	stoney gravel	0.14	-69
42	Wanaka	3.7	loamy sand	0.41	-15
43	Hanmer	3.3	silt loam	0.4	-40
44	Eyrewell - Downs	3.2	stoney/sandy loam	0.42	-59
45	Dunsandel	2.9	stoney silt loam	0.32	-62
46	Crown Range	1.8	silt loam	0.22	-25
47	Dunback	1.5	silt loam	0.36	-18
48	Tara Hills	1.2	sandy loam	2.1	-64
49	Dunedin	1.2	silt loam	1.15	-19
50	Glynn Wye	1.1	silt loam	0.44	-24
51	Hororata -West	0.9	stoney silt loam	0.33	-25
52	Low Mount	0.0	silt loam	0.23	-20

Appendix E

Long-term mean minimum February and May temperature recorded at 260 climate recording stations across New Zealand. Data were taken from the reference New Zealand Meteorological Service 1983.

No	Station name	Latitude	Longitude	Altitude	February temp.	May temp.
1	Mokohinau	35°54S	175°07E	102	17.4	13.1
2	Mechanics Bay	36°51S	174°47E	4	17	11.4
3	Leigh	36°16S	174°48E	27	16.4	11.9
4	Cape Reinga	34°25S	172°41E	191	16.4	11.0
5	East Cape	37°42S	178°33E	17	16.1	8.4
6	Aupouri forest	35°01S	173°12E	69	16.1	12.1
7	Auckland airport	37°01S	174°48E	8	15.8	9.7
8	Takatu, Matakana	36°22S	174°46E	70	15.7	10.9
9	Kaitaia airport	35°04S	173°17E	80	15.7	11.0
10	Waitangi forest	35°15S	174°04E	55	15.3	9.7
11	Thames	37°08S	175°32E	3	15.3	9.1
12	Port Fitzroy	36°11S	175°22E	4	15.2	10.8
13	Omata	39°05S	174°00E	61	15	8.5
14	Mokau	38°43S	174°37E	46	14.9	9.4
15	Whangarei airport	35°46S	174°22E	37	14.9	9.5
16	Opotiki	38°00S	177°17E	6	14.7	7.4
17	Te Paki Station	34°30S	172°48E	64	14.7	10.5
18	Castlepoint	40°54S	176°13E	3	14.6	9.5
19	Brightlands Bay	41°04S	173°51E	15	14.6	10.0
20	Tairua forest	37°10S	175°51E	3	14.6	8.2
21	Kaitaia	35°07S	173°61E	8	14.6	9.8
22	Woodhill forest	36°45S	174°26E	30	14.6	9.6
23	Kaikohe	35°25S	173°49E	204	14.5	10.1
24	Pukekohe	37°12S	174°52E	82	14.5	9.1
25	Maioro forest	37°21S	174°43E	52	14.4	9.2
26	Cape Palliser	41°37S	175°18E	10	14.3	9.9
27	Kerikeri	35°14S	173°57E	73	14.2	9.1
28	Napier airport	39°30S	176°55E	2	14.1	6.5

29	Te Kauwhata	37°25S	175°08E	32	14.1	8.1
30	Edgecumbe	37°59S	176°50E	5	14.0	6.6
31	Kawerau	38°05S	176°43E	30	14.0	6.7
32	Wellington airport	41°20S	174°49S	6	14.0	9.0
33	Cape Egmont	39°17S	173°45S	8	14.0	9.6
34	Paerata	37°09S	174°54S	46	14.0	9.0
35	Warkworth	36°26S	174°40E	72	13.9	8.9
36	Whenuapai	36°47S	174°38E	26	13.9	8.6
37	Dargaville	35°57S	173°50E	20	13.9	9.3
38	Tauranga airport	37°41S	176°10E	2	13.8	7.4
39	Paeroa	37°23S	175°40E	4	13.8	7.1
40	Wanganui	39°56S	175°03E	22	13.8	8.0
41	Te Puke	37°49S	176°19E	91	13.8	8.0
42	Cape Campbell	41°44S	174°17E	3	13.7	8.7
43	Puketurua	35°40S	174°05E	101	13.7	8.6
44	Tangoio	39°18S	176°52E	213	13.7	8.3
45	Ruatoria	37°54S	178°19E	61	13.7	7.3
46	Umawera No 2	35°18S	173°33E	64	13.7	8.5
47	Patea	39°45S	174°28E	43	13.6	8.9
48	Te Aroha	37°33S	175°43E	18	13.6	7.1
49	New Plymouth	39°04S	174°05E	49	13.6	8.9
50	Waihi	37°23S	175°51E	91	13.5	7.2
51	Frasertown, Wairoa	39°00S	177°24E	8	13.5	6.8
52	Lake Grassmere	41°44S	174°09E	2	13.5	6.8
53	Whatawhata	37°49S	175°05E	104	13.4	7.6
54	Moutere Hills	41°21S	173°04E	110	13.4	7.3
55	Rukuhia	37°50S	175°18E	66	13.4	7.1
56	Whakatane airport	37°55S	176°55E	6	13.4	5.3
57	Whangapoua forest	36°46S	175°36E	4	13.4	7.9
58	Gisborne airport	38°40S	177°59E	4	13.3	7.1
59	Te Teko	38°02S	176°49E	8	13.3	6.0
60	Wharekawa	37°09S	175°51E	15	13.3	7.5
61	Taradale	39°32S	176°51E	5	13.2	6.7
62	Waimana	38°09S	177°05E	37	13.2	4.3

63	Waipoua forest	35°39S	173°33E	88	13.1	8.5
64	Kelburn Wellington	41°17S	174°46E	125	13.1	8.2
65	Ardmore	37°02S	174°58E	30	13.1	7.7
66	Avalon, Low Hutt	41°11S	174°58E	65	13.0	7.5
67	Ohakea	40°12S	175°23E	48	13.0	7.2
68	Farewell Spit	40°33S	173°01E	3	13.0	7.7
69	Paraparaumu airport	40°54S	174°59E	7	13.0	7.4
70	Levin	40°39S	175°16E	46	12.9	7.2
71	Arapuni power station	38°04S	175°39E	123	12.9	6.0
72	Pauatahanui	41°07S	174°54E	30	12.9	7.9
73	Palmerston North, DSIR	40°23S	175°37E	34	12.8	6.8
74	Porirua	41°09S	174°51E	94	12.7	7.6
75	Te Kuiti	38°20S	175°09E	61	12.7	6.0
76	Greymouth	42°28S	171°12E	4	12.7	7.3
77	Flockhouse	40°14S	175°16E	9	12.7	6.5
78	Mt Pleasant	43°34S	172°43E	137	12.7	7.3
79	Glenbervie forest	35°39S	174°21E	107	12.6	7.5
80	Mangatu forest	38°17S	177°51E	182	12.6	6.2
81	Riverhead forest	36°46S	174°35E	28	12.6	7.4
82	Hastings	39°39S	176°51E	14	12.6	5.1
83	Ngatea	37°16S	175°31E	2	12.6	6.3
84	Rotoehu forest	37°54S	176°31E	72	12.6	5.3
85	Waerenga O Kuri	38°41S	177°48E	314	12.5	6.9
86	Cambridge	37°55S	175°30E	76	12.5	6.2
87	Appleby	41°17S	173°06E	17	12.5	5.4
88	Bromley, Christchurch	43°32S	172°42E	9	12.5	5.7
89	Murupara	38°27S	176°42E	198	12.5	3.4
90	Maramarua forest	37°18S	175°15E	38	12.5	6.6
91	Nelson airport	41°17S	173°14E	2	12.4	4.5
92	Nelson	41°17S	173°18E	10	12.4	5.7
93	Te Marua	41°06S	175°06E	84	12.4	4.5
94	Makara	41°15S	174°42E	279	12.4	7.9
95	Kaikoura	42°25S	173°42E	108	12.4	7.3
96	Tangimoana	40°18S	175°15E	2	12.3	6.2

97	Rotorua airfield	38°10S	176°16E	297	12.3	6.0
98	Westport airport	41°44S	171°35E	2	12.3	7.2
99	Waikeria	38°07S	175°24E	46	12.3	4.8
100	Kaweka forest	39°26S	176°28E	414	12.3	7.0
101	Onawe, Duvauchelle Bay	43°46S	172°56E	46	12.2	6.7
102	Taumarunui	38°52S	175°16E	171	12.1	4.8
103	Wither Hills, Blenheim	41°32S	173°57E	32	12.1	5.4
104	Hokio Beach School	40°36S	175°12E	6	12.1	6.4
105	Manaia Dem. Farm	39°32S	174°09E	98	12.1	7.4
106	Havelock North	39°40S	176°53E	9	12.0	4.4
107	Dannevirke	40°13S	176°07E	207	12.0	6.1
108	Waiorongamai	41°16S	175°09E	21	12.0	6.6
109	Blenheim airport	41°31S	173°52E	27	12.0	4.8
110	Marton	40°05S	175°25E	141	11.9	6.1
111	Tarawera forest	38°08S	176°39E	61	11.9	3.8
112	Wainuiomata	41°17S	174°57E	82	11.9	6.5
113	Ruakura, Hamilton	37°47S	175°19E	40	11.9	5.9
114	Esk forest	39°15S	176°42E	427	11.9	6.0
115	Mangamutu, Pahiatua	40°27S	175°49E	116	11.8	5.6
116	Tokoroa	38°13S	175°52E	305	11.8	4.5
117	Hokitika airport	42°43S	170°59E	39	11.7	5.5
118	Onepoto, Waikaremoana	38°48S	177°07E	643	11.7	5.9
119	Rata Farm, Te Uri	40°16S	176°23E	488	11.7	6.5
120	Putaruru	38°07S	175°40E	155	11.7	5.7
121	Otutira	38°38S	175°49E	579	11.7	3.9
122	Riwaka, Motueka	41°06S	172°58E	8	11.6	4.5
123	Upokopoito	39°45S	175°09E	34	11.6	3.8
124	Mohaka forest	39°04S	177°02E	286	11.6	6.3
125	Christchurch airport	43°29S	172°32E	30	11.6	3.9
126	Waipukurau	40°00S	176°32E	137	11.5	5.1
127	Wallaceville	41°08S	175°03E	56	11.5	5.6
128	Karori, Wellington	39°29S	175°31E	648	11.5	6.8
129	Wairakei power station	38°38S	176°06E	342	11.5	4.8
130	Wigram aero	43°33S	172°33E	22	11.4	4.0

131	Turangi	39°00S	175°48E	366	11.4	4.6
132	Taupo	38°41S	176°04E	376	11.4	4.9
133	Tauherenikau, Alloa	41°07S	175°23E	43	11.3	5.8
134	Kopua	40°05S	176°17E	311	11.2	5.4
135	Taiaroa Head	45°47S	170°44E	72	11.2	6.7
136	Greytown	40°54S	176°13E	3	11.2	5.2
137	Lake Hawea	44°37S	169°15E	350	11.1	3.1
138	Bagshot Station	40°52S	175°46E	171	11.0	5.0
139	Stratford Dem. Farm	39°20S	174°18E	311	11.0	6.1
140	Vernon Lagoons	41°32S	174°02E	2	11.0	4.1
141	Musselburgh, Dunedin	45°54S	170°31E	2	11.0	5.5
142	Oamaru, Iona Hospital	45°04S	171°00E	14	11.0	5.3
143	Waipara	43°04S	172°45E	64	10.9	4.3
144	Haast	43°52S	169°00E	4	10.9	6.2
145	Jacksons Bay	43°59S	168°37E	8	10.9	6.2
146	Gladstone, Arahura	41°08S	175°38E	116	10.9	5.2
147	Ashley Forest	43°15S	172°35E	107	10.9	5.1
148	East Taratahi	41°01S	175°37E	91	10.9	5.0
149	Adair	44°26S	171°10E	85	10.9	4.7
150	The Jordan, Awatere Valley	41°49S	173°46E	305	10.8	4.0
151	Lincoln	43°39S	172°28E	11	10.8	4.0
152	Waingawa, Masterton	40°59S	175°37E	114	10.8	4.9
153	Timaru	44°25S	171°15E	17	10.8	3.6
154	Tiwai Point, Bluff	46°35S	168°23E	5	10.8	5.6
155	Lower Retaruke	39°04S	175°12E	223	10.8	4.6
156	Waihope Power Station	41°40S	173°34E	262	10.7	3.7
157	Te Wera Forest	39°14S	174°36E	180	10.6	4.6
158	Mount Bruce Reserve	40°43S	175°38E	305	10.6	4.9
159	Minginui Forest	38°39S	176°44E	366	10.6	2.5
160	Hari hari	43°09S	170°33E	45	10.6	3.0
161	Franz Josef	43°23S	170°11E	122	10.6	4.9
162	Makaretu	39°57S	176°19E	335	10.6	5.1
163	Reefton	42°07S	171°52E	198	10.6	3.4
164	Cromwell	45°02S	169°12E	213	10.6	1.2

165	Waimate	44°44S	171°03E	61	10.5	1.4
166	Ashburton	43°54S	171°45E	101	10.5	3.1
167	Wanaka	44°42S	169°08E	296	10.4	1.7
168	Milford Sound	44°40S	167°55E	3	10.4	4.3
169	Alexandra	45°16S	169°23E	141	10.3	0.9
170	Kaitoke	41°05S	175°11E	223	10.3	2.8
171	Pureora Forest	38°31S	175°33E	549	10.3	4.1
172	Kaingaroa Forest	38°24S	176°34E	544	10.3	3.6
173	Rangiora	43°19S	172°34E	46	10.3	3.5
174	Highbank Power St.	43°35S	171°44E	336	10.2	4.4
175	Rakaia	43°45S	172°02E	106	10.2	3.1
176	Oamaru Airport	44°58S	171°05E	30	10.2	3.7
177	Nugget Point	46°27S	169°49E	129	10.2	5.6
178	Rai Valley	41°14S	173°35E	79	10.2	3.9
179	Mangahao Upper	41°09S	174°51E	94	10.2	4.9
180	Winchmore	43°48S	171°48E	160	10.1	3.0
181	Murchison	41°48S	172°20E	158	10.1	4.3
182	Totora Flat	42°18S	171°37E	77	10.1	3.6
183	Darfield	43°29S	172°08E	195	10.0	3.1
184	Eyrewell Forest	43°24S	172°17E	158	10.0	2.8
185	Kuripapango	39°24S	176°20E	488	10.0	3.4
186	Ngaumu Forest	41°02S	175°53E	244	10.0	4.4
187	Temuka	44°15S	171°17E	24	9.9	3.0
188	Otira	42°50S	171°34E	383	9.9	3.4
189	Fox Glacier	43°28S	170°01E	152	9.9	4.1
190	Orari Estate	44°08S	171°19E	81	9.8	2.4
191	Wairapukao Forest	38°32S	176°34E	437	9.8	1.8
192	Rudstone	43°33S	171°41E	371	9.8	4.1
193	Timaru Airport	44°18S	171°14E	26	9.8	2.4
194	Balmoral Forest	42°52S	172°45E	198	9.7	1.9
195	Waiau	42°39S	173°03E	137	9.7	2.5
196	Gwavas Forest	39°44S	176°27E	335	9.7	4.1
197	Hororata Substation	43°33S	171°59E	192	9.7	2.4
198	Lake Coleridge	43°22S	171°32E	364	9.6	-0.6

199	Pukahunui	38°44S	176°31E	668	9.6	2.9
200	West Arm, Manapouri	45°31S	167°16E	180	9.6	3.8
201	Waiotapu Forest	38°19S	176°25E	435.0	9.5	2.6
202	Golden Downs Forest	41°33S	172°53E	274.0	9.5	2.0
203	Roxborough Power St.	45°29S	169°19E	110.0	9.4	3.0
204	Geraldine	44°06S	171°14E	119.0	9.3	2.3
205	Taieri Mouth	46°05S	170°12E	15.0	9.3	4.6
206	Waimihia Forest	38°50S	176°16E	743.0	9.3	2.5
207	Cherry Farm Hospital	45°37S	170°37E	6.0	9.2	1.1
208	Balclutha	46°16S	169°44E	6.0	9.2	3.6
209	Ikawai	44°52S	170°56E	70.0	9.2	2.4
210	Queenstown Airport	45°01S	168°44E	349.0	9.1	1.5
211	Taihape	39°41S	175°48E	433.0	9.1	3.8
212	Gore, DSIR	46°06S	168°56E	72.0	8.9	3.8
213	Invermay	45°51S	170°22E	24.0	8.9	2.7
214	Berwick Forest	45°58S	170°04E	18.0	8.9	2.9
215	Milton	46°07S	169°58E	18.0	8.9	3.0
216	Hanmer	42°31S	172°51E	387.0	8.9	1.6
217	Gore	46°07S	168°54E	123.0	8.8	3.4
218	Peel Forest	43°54S	171°16E	274.0	8.8	1.9
219	Makahu Saddle	39°17S	176°24E	974.0	8.7	3.3
220	Winton	46°09S	168°20E	44.0	8.7	3.5
221	Earnscleugh	45°14S	169°20E	152.0	8.7	-0.2
222	Dunedin Airport	45°56S	170°12E	1.0	8.7	2.3
223	Palmerston	45°29S	170°43E	21.0	8.7	2.3
224	Hokonui Forest	46°13S	168°35E	46.0	8.6	3.3
225	Invercargill Airport	46°25S	168°20E	0.0	8.6	3.0
226	Lake Pukaki	44°11S	170°08E	556.0	8.5	0.1
227	Karioi	39°29S	175°31E	648.0	8.5	2.7
228	Herbert Forest	45°15S	170°46E	61.0	8.5	2.8
229	Ohakune	39°24S	175°25E	610.0	8.5	3.6
230	Ophir	45°07S	169°37E	305.0	8.4	-0.7
231	Woodlands	46°22S	168°36E	47.0	8.4	3.9
232	East Gore	46°05S	168°57E	75.0	8.4	2.4

233	Wharite Peak	40°15S	175°51E	914.0	8.4	3.6
234	Tara Hills, Omarama	44°32S	169°54E	488.0	8.4	0.2
235	Cobb Dam	41°06S	172°41E	823.0	8.4	2.0
236	Lake Rotoiti	41°48S	172°51E	634.0	8.3	1.2
237	Rankleburn Forest	45°58S	169°26E	255.0	8.3	3.3
238	Otautau	46°10S	168°00E	55.0	8.3	2.7
239	Mid-Dome	45°34S	168°30E	386.0	8.3	2.1
240	Mount John	43°59S	170°28E	1027.0	8.3	1.5
241	Hermitage, Mt Cook	43°44S	170° 06E	765.0	8.3	0.8
242	Waiouru	39°28S	175°40E	823.0	8.1	0.8
243	Stratford Mt. House	39°18S	174°07E	846.0	8.1	3.4
244	lake Tekapo	44°01S	170°28E	683.0	8.1	0.7
245	Fairlie	44°06S	170°49E	306.0	8.1	-0.1
246	Te Anau	45°25S	167°44E	215.0	8.0	2.2
247	Waipiata	45°14S	170°08E	472.0	8.0	0.6
248	Owaka	46°27S	169°40E	5.0	7.9	3.5
249	Mahinerangi Dam	45°53S	169°58E	396.0	7.9	2.5
250	Twizel	44°15S	170°06E	457.0	7.8	-0.5
251	Moa Flat	45°46S	169°17E	410.0	7.7	2.2
252	Hindin Farm	45°45S	170°12E	455.0	7.7	2.3
253	Tapanui	45°57S	169°17E	226.0	7.6	2.3
254	Chateau, Mt Ruapehu	39°12S	175°32E	1119.0	7.3	1.7
255	Craigieburn Forest	43°09S	171°43E	914.0	7.2	0.5
256	Molesworth	42°05S	173°16E	893.0	6.8	-0.3
257	Moa Creek	45°11S	169°39E	427.0	6.6	-1.8
258	Ranfurly	45°08S	170°06E	427.0	6.5	0.2
259	Naseby	45°01S	170°06E	610.0	6.4	-0.3
260	Manorburn Dam	45°22S	169°36E	746.0	5.9	-1.0

Appendix F

The long term annual temperatures for Kulani camp, Hawaii. The station is at an altitude of 1550m. The data presented are the mean values for recordings from 1949 to 1994: supplied by Western Regional Climate Centre, Desert Research Institute, Nevada, USA.

Month	Temperature (°C)		
	Maximum	Minimum	Mean
January	16.7	6.1	11.3
February	16.5	6.2	11.4
March	16.0	6.8	11.4
April	16.3	7.7	12.0
May	16.8	8.4	12.6
June	17.9	10.7	13.4
July	18.4	9.8	14.1
August	18.7	9.9	14.3
September	18.7	9.8	14.3
October	18.6	9.5	14.1
November	17.6	8.6	13.1
December	16.8	7.1	12.0

Appendix G

The mean temperature of the warmest and coldest months for the Ano Nuevo natural stand of radiata pine in the Northern Hemisphere and comparable North Auckland sites in New Zealand in the Southern Hemisphere. The data for Ano Nuevo (represented by the Ben Lomond meteorological station) were taken from Sweet (1981). The New Zealand data were taken from the reference New Zealand Meteorological Service (1983).

Site	Latitude	Altitude (m)	Mean temperature warmest month (°C)	Mean temperature coldest month (°C)
Ben Lomond	37°05'N	473.6	18.2	7.0
Mokohinau	35°54'S	102.0	20.6	12.6
Glenbervie	35°39'S	107.0	18.0	9.5